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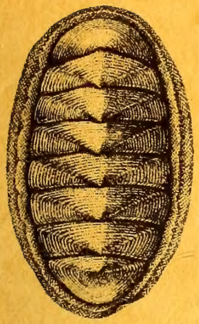

AMERICAN MALACOLOGICAL BULLETIN

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Cover. A dorsal view of *Chiton fosteri* Bullock from Oman. This and other chitons from Oman and the Arabian Gulf are discussed in a paper by Kaas and Van Belle in this issue. This paper is one in a series of papers that appear herein as part of the proceedings of the 1987 American Malacological Union Symposium on the Biology of the Polyplacophora.

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January 1988

A COMPARISON OF GROWTH RATE BETWEEN SHALLOW WATER AND DEEP WATER POPULATIONS OF SCALLOPS, *PLACOPECTEN MAGELLANICUS* (GMELIN, 1791), IN THE GULF OF MAINE

DANIEL F. SCHICK, SANDRA E. SHUMWAY
AND
MARGARET A. HUNTER
DEPARTMENT OF MARINE RESOURCES
WEST BOOTHBAY HARBOR, MAINE 04575, U. S. A.

ABSTRACT

The rate of growth over several years has been compared between two shallow water (13-20 m) and two deep water (170 m) populations of the sea scallop *Placopecten magellanicus* (Gmelin). Scallops from one shallow water population were tagged and released in 1977 for fishermen to recapture. Additional scallops from a nearby population were tagged in 1978 for periodic retrieval and measurement by divers over a subsequent four year period. The deep water scallops were sampled periodically over eight years (1976-1983), and their growth was measured through analysis of height-frequency of an anomalously numerous year class spawned in 1975. The rate of growth of the offshore, deep water scallops was found to be less than that of the inshore, shallow water scallops. The calculated maximum sizes attained, as determined by Ford-Walford plots are 150 mm for the shallow water populations and 110 mm for the deep water populations.

The giant scallop, *Placopecten magellanicus* (Gmelin), is of considerable economic importance in eastern Canada and the northeastern United States and has thus been the subject of a number of growth studies (Stevenson, 1936; Chaisson, 1949; Welch, 1950; Stevenson and Dickie, 1954; Haynes, 1966; Merrill *et al.,* 1966; Naidu, 1969, 1975; Jamieson, 1979; Posgay, 1979; Posgay and Merrill, 1979; Ehinger, 1982; Serchuk *et al.,* 1982; Serchuk and Rak, 1983; Choinard, 1984; Krantz *et al.,* 1984; Mohn *et al.,* 1984; MacDonald and Thompson, 1985; Roddick and Mohn, 1985). In all but five of these studies, age was estimated and growth was determined by the method of Merrill *et al.* (1966) i.e. counting shell rings and resilifer lines. Estimates of growth have also been made by measuring increasing weight of somatic tissue using either the adductor muscle (Haynes, 1966; Serchuk and Rak, 1983; Mohn *et al.,* 1984) or whole somatic tissue dry weight (MacDonald and Thompson, 1985). Krantz *et al.* (1984) estimated growth by measuring temperature-induced changes in $^{18}O/^{16}O$ ratios in the scallop shell calcite. Only Posgay (1963) and Naidu (1975) have measured growth through tagging and recovery thus validating age determination in the species. None of the above studies include data that show the effects of handling by repeated measurements of shell growth of scallops *in situ.*

Variations in a number of allometric relationships with depth for sea scallops have been observed (Schick *et al.,* 1987) and depth as a factor in scallop growth has been addressed previously by a number of authors (Caddy *et al.,* 1970; Posgay, 1979; MacDonald and Thompson, 1985). Posgay (1979) has noted a decrease in growth with increasing water depth for scallops on Georges Bank at four ranges between 55 and 109 m. Caddy *et al.* (1970), however, found little variation at five depth ranges between 55 and 144 m in the Bay of Fundy. MacDonald and Thompson (1985) studied growth at 10, 20, and 31 m off Newfoundland, Canada and found decreasing growth with increasing depth.

In the present study, scallops were collected from two shallow water populations (13-20 m) along the Maine coast and two deep water populations (170 m) in the Gulf of Maine to determine the extent to which the rate of growth varied with depth.

MATERIALS AND METHODS

Specimens of the sea scallop, *Placopecten magellanicus,* were collected from two shallow water and two deep-water locations in the Gulf of Maine for age and growth determinations (Fig. 1). The shallow-water animals were collected from Jericho Bay, Maine (44°11.5′N, 68°30′S), using an eight foot wide (2.4 m), three gang commercial drag in tows of 10 minutes duration. Intact animals were measured for shell height and length (Fig. 2) and then tagged by drilling a hole through the upper valve over the byssal notch area and inserting a Floy polyethylene spaghetti tag secured with knots. Other workers have demonstrated that this method of tagging is not harmful to the scallops (Posgay, 1963, 1981; Naidu and Cahill, 1985). Scallops were held out of the water for a maximum of three minutes during the tagging process and were held in running seawater tanks prior to release to minimize stress. In June 1977, 1000 scallops were broadcast over commercial fishing grounds in Jericho Bay, an area with depths ranging from 13-20 m identified by fishermen as being good scallop grounds. Tags and shells were returned by fishermen over the next three years.

Another shallow water collection of scallops was obtained in June 1978 by divers near Ringtown Island, Maine (44°07.4′N , 68°29.4′S) an island just south of Jericho Bay. These scallops were tagged, measured and placed by divers in an area protected from dragging by rough bottom conformation. They were subsequently recovered, remeasured and released in November 1978, June 1979, December 1981 and finally recaptured in June 1982 yielding the first scallop growth data showing the effects of repeated handling.

In both shallow water scallop groups, growth was determined by measuring the increase in tangential shell height of the left (top) valve between the time of tagging and time of recapture as well as measuring the height of rings formed during that time (Naidu, 1975; Posgay, 1981). Shell height at age was determined using the technique of Merrill *et al.* (1966) and a table of mean height-at-age was constructed for both groups. Since ring formation occurs during the winter and scallops spawn in the late summer, the age at first ring formation is taken as 6 months with subsequent rings found at 18 months, 30 months, etc.

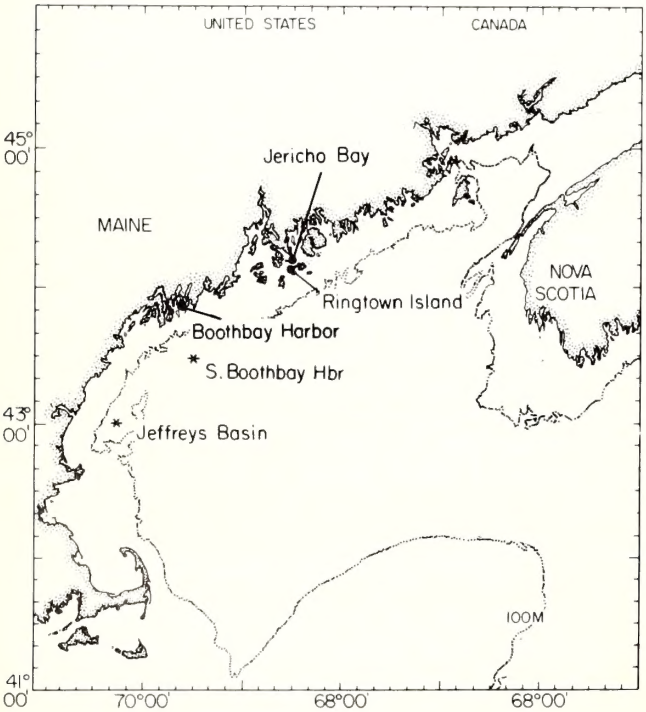

Fig. 1. Location of shallow water and deep water sea scallop sampling sites in the Gulf of Maine.

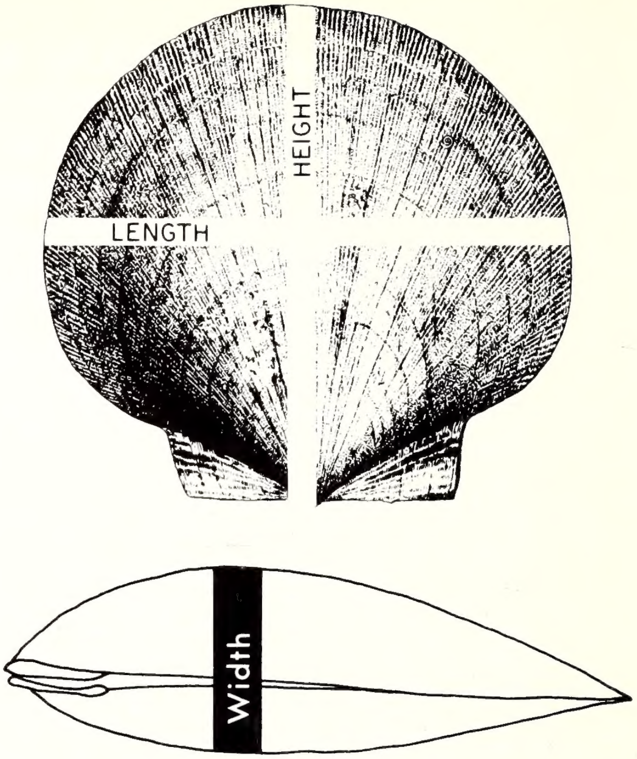

Fig. 2. Sea scallop shell conformation and dimensions.

Deep water scallops from 170 m depth in the Gulf of Maine were collected annually in August using a fine mesh, 32 ft. (9.8 m) chain footrope, semi-balloon otter trawl. Two deep water locations provided continuous records between 1976 and 1983 except in 1980 when samples were unavailable. These were: ∿32 km (20 miles) South of Boothbay Harbor (43°26.5′N, 69°33.3′S) and Jeffrey's Basin (43°04.25′N, 70° 11.33′S). Height frequency distributions over time were determined from shell heights measured to the nearest millimeter (Figs. 3, 4). The increment in shell height of a predominant year class (1975) from one year to the next was used as a measure of growth. The shell heights are for August, and since scallops spawn in August, the first height frequency is taken as scallops at one year of age, with subsequent annual collections representing scallops at 2 years, 3 years, etc. This assumption of age is based on examination of the shells from the first sample which showed one ring on each shell indicating that they had survived one winter.

Controversy still exists over the most accurate method of determining the correct age of scallops (Merrill *et al.*, 1966; Krantz *et al.*, 1984). Unfortunately, our data do little to clarify the situation. In four of the five shells of scallops retrieved alive during the second year after the Jericho Bay tag releases, there was one more ring than there should have been between the file mark and the leading edge. These shells should have contained one ring with growth before and after the ring. Instead they contained two rings with growth after the second ring. This happened in a small number of returns, but did occur in four of the five specimens, indicating perhaps more than a chance occurrence. No evidence of shell margin chipping or other damage was apparent in the shells to indicate the possibility of one of the rings being a shock mark. None of the 93 first year tag returns showed any ring formation. What caused the two rings to form in four of the five living second year tag returns is unknown. Approximately 25 scallops from the general area that were tagged and sequentially retrieved by divers over four years showed exact correlation between numbers of years and number of rings.

The offshore, deep water scallops, identified as essentially one single year class, were sampled annually and a height frequency histogram over time in the form of a 3-dimensional diagram was prepared. This histogram shows a single size mode through time. Scallops from a 1980 collection were read for shell ring structure by ten investigators. Considerable variation in numbers of rings per shell occurred between readers. The combined observed age distribution of 43 scallops from the same year class read by 10 readers was 5 at four years, 73 at five years, 237 at six years, 102 at seven years, and 13 at eight years. The problems of ring identification and the variety of aids including corroboration by resilifer marks have been addressed by Merrill *et al.* (1966) and still exist today. Also, the time from spatfall to the first readable ring, usually around 25 mm, is open to question, further clouding the relationship between a scallop's size and age.

Two problems arise in comparing the ring-structure method of age determination with the ^{18}O to ^{16}O ratio in the shell calcite method of Krantz *et al.* (1984). First, the ratio work was only performed on two shells. Second, age determination of these shells was by the method of Merrill *et al.* (1966) in which two readers agreed on age. There is enough discrepancy in age determination between the two methods to very probably negate any chance of the misreading of rings causing the difference in age. Still, the unknowns of exact age on both sides of the comparison leave the whole question open to more definitive research being needed. Our first year tag returns and our diver-retrieved aging results seem to support the one ring one year theory, yet the second year returns from the fishermen support the more than one ring per year theory of Krantz *et al.* (1984). Our offshore shells seem to indicate one ring-one year, but the reader error or perhaps the true ring number variation indicates the age determination process is still inexact.

Ford-Walford plots were constructed from shell increment measurements taken from shallow water (Ringtown) scallops to obtain an estimate of the von Bertalanffy growth equation parameters H∞ and k. Ford-Walford plots were also constructed for the deep water population at 32 km south of Boothbay Harbor using the annual growth increments in the predominant (1975) year class. The parameters H∞, k, and t_o for the von Bertalanffy growth equation, $H_t = H\infty (1 - e^{-k(t-t_o)})$, were determined from the height and age data for both the shallow-water and deep-water populations. A computer model was employed that uses an iterative process to scan a grid of options for the parameters H-infinity, k and t_o for a least-squares fit given age-length data (Allen, 1966) and calculates asymptotic confidence intervals for each parameter (Ralston and Jennrich, 1978). All calculations were carried out on an IBM 370 computer.

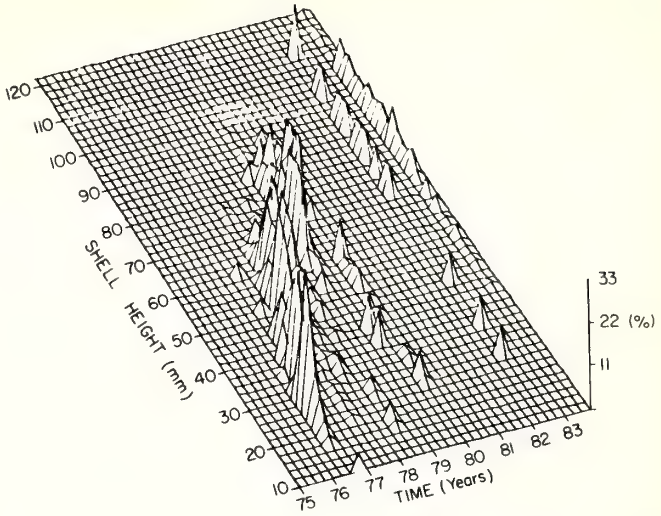

Fig. 3. Three-dimensional plot of shell height frequencies vs. time from a deep water sea scallop population located 32 km south of Boothbay Harbor, Maine.

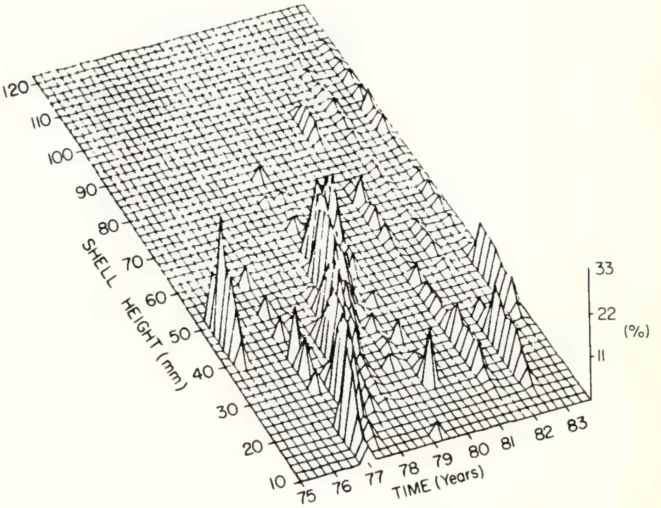

Fig. 4. Three-dimensional plot of shell height frequencies vs. time from a deep water sea scallop population located west of Jeffrey's Ledge in the Gulf of Maine.

Measuring growth by ring deposition in survivors of a year class can be subject to a bias known as Lee's Phenomenon (Lee, 1912) where the results depend on selection factors in mortality of that year class. Selection factors can favor slower growing scallops by killing off the faster growing individuals at a higher rate than the slower growing, smaller individuals. If this occurs, then the mean size at age of the survivors will be smaller than the mean size at age of the year class without the selecting factor and the resulting lag in mean size at age will bias the growth curve. Fishing mortality is such a factor. If the fishing gear selection is for taking larger individuals, the smaller scallops of any one year class will be more likely to survive, producing a growth curve that tails off faster than it should. In terms of von Bertalanffy parameters, the iterative process could be forced to select an H-infinity that is lower than it should be and that will force the selection of a k value that is higher than it should be. Due to the possibility of Lee's Phenomenon from a variety of factors, fishing mortality, handling of scallops, etc., it is dangerous to look at only one parameter from a von Bertalanffy curve and state that it is higher or lower than the same parameter from another curve and attach any significance to the comparison since all three of the parameters are related and interactive.

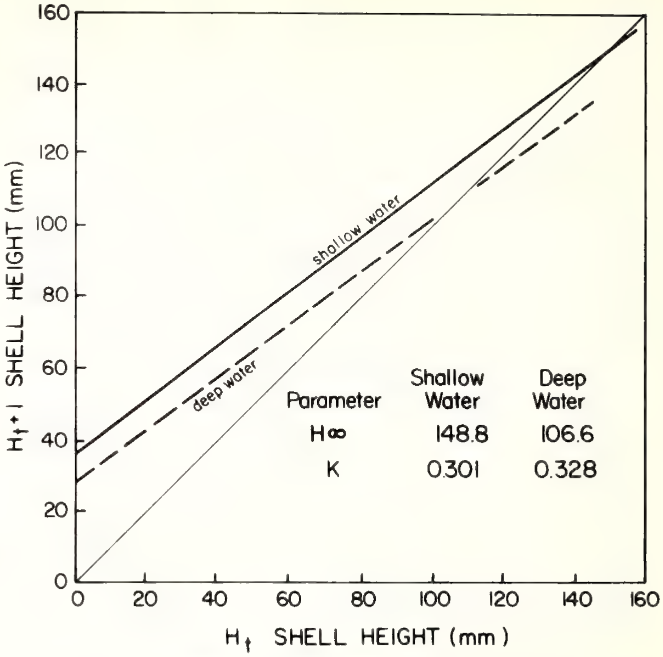

Fig. 5. Shallow water and deep water Gulf of Maine sea scallop growth: Ford-Walford plots and derived von Bertalanffy parameters.

RESULTS

Growth rates for four populations of *Placopecten magellanicus* were determined. Mean shell height at age was calculated for each shallow-water population from the shell ring measurements (Table 1) and the same was calculated for each deep-water population from the height frequency of the one predominant year class measured annually (Table 2). The same data were used to determine the von Bertalanffy growth parameters and the asymptotic confidence intervals for all four populations (Table 3).

Ford-Walford plots for the Ringtown Island population and for the 32 km south of Boothbay Harbor population indicate an H-infinity of 150 mm and 110 mm respectively (Fig. 5) which agrees closely with the empirical data (Tables 1, 2). Further evidence for the growth rate difference is illustrated in figure 6 which shows the von Bertalanffy growth curves for each of the four populations. Note that the Ringtown Island population gives a slightly lower curve than does the Jericho Bay population, but both are higher than the curves for the two deep-water populations.

In the von Bertalanffy growth equation, the parameters H-infinity and k are inversely related. At the 32 km south of Boothbay Harbor station, a heavy fishery for scallops in that area cropped off the larger scallops starting in 1981, making what appeared to be the predominant year class in the last two years' length-frequencies artificially low. An attempt to separate the year classes in the length-frequencies for 1982-1983 by NORMSEP (Hasselblad, 1966) failed, so the predominant bump was used *in toto* for both years. When the iterative process in Allen's (1966) fit of von Bertalanffy parameters to the data was attempted, it found a better fit with

Table 1. Age-at-height key for shallow water scallops. Data generated from measured rings. Heights are given in mm.

	AGE IN YEARS									
LOCATION	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
Jericho Bay	11.4	39.3	63.7	88.7	110.2	123.5	135.7	—	—	—
Ringtown Island			71.0	90.7	101.1	110.0	122.3	128.2	136.5	140.0

Table 2. Age-at-height key for deep-water scallops. Data generated from height-frequency data. Heights are given in mm.

	AGE IN YEARS							
LOCATION	1.0	2.0	3.0	4.0	5.0	6.0	7.0	8.0
32 km South Boothbay Harbor	27.2	51.4	64.1	75.9	—	—	101.0	103.6
W. Jeffreys Ledge	25.9	41.2	57.5	—	90.6	96.7	103.1	—

Table 3. Least squares regressions of Von Bertalanffy parameters for scallops from 4 locations in the Gulf of Maine. Values are ± 1 Asymptotic Confidence Interval.

Location	Depth (m)	H∞	K	T_O	Years fitted
Shallow Water					
Jericho Bay	25	248 ± 47.9	0.13 ± 0.036	0.17 ± .095	1-8
Ringtown Island	15	148 ± 7.7	0.27 ± 0.059	0.10 ± 0.494	1-9
Deep Water					
S. Boothbay Harbor	170	116 ± 3.7	0.28 ± 0.025	−0.01 ± 0.103	1-8
W. Jeffrey's Ledge	174	223 ± 35.3	0.09 ± 0.019	−0.37 ± 0.110	1-7

the lower H-infinity, and this raised the k value. The von Bertalanffy parameters (Table 3) and the curve (Fig. 6) for the 20 miles south of Boothbay Harbor scallop data reflects this with a more rapid rise (higher k) in early years and with a tailing off (lower H-infinity) in later years compared to the Jeffrey's Basin data.

The Ringtown Island scallops were measured by repeatedly collecting them, bringing them to the surface, measuring them and returning them to the bottom. This amount of handling could have retarded their growth in the years during the measurements. Chapman (pers. comm.) and Naidu (pers. comm.) have both indicated that handling, even slight handling in an aquarium situation, can retard shell deposition. The von Bertalanffy curve for the Ringtown Island scallop data shows good growth in the early years, before the scallops were caught, and much slower growth in the last few years. The salient point is that even with the possibility of retarded growth due to repeated handling, the Ringtown Island scallop growth is still greater than the growth of the deep-water scallops. Note that the shallow water growth curves are based on annual increments beginning at six months of age whereas the deep water growth curves are based on annual increments beginning at one year of age. The scallops sampled ranged in age from one to nine years.

DISCUSSION

The data presented here clearly demonstrate a marked difference in growth rate between shallow water and deep water scallop populations and also represents the first *in situ* study of the effects of handling on growth of scallops. Our data are in general agreement with previously published growth data for *Placopecten magellanicus* and further support the theory that growth is depth dependent, with increasing depth representing deteriorating environmental suitability.

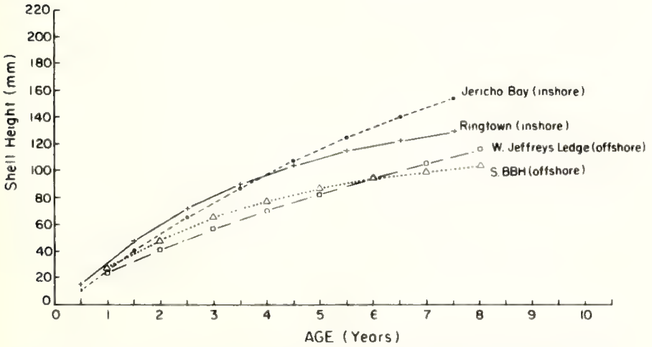

Fig. 6. Von Bertalanffy growth curves for two shallow water and two deep water sea scallop populations in the Gulf of Maine.

A number of authors have reported on growth rates in *Placopecten magellanicus* and their results are briefly summarized here only as they apply to the present study. Welch (1950), in one of the earliest studies of growth in this species, reported height-at-age measurements for scallops from Jericho Bay, the same area used in the present investigation. His reported average values of 46.3 mm for the second ring and 142.2 mm for the ninth ring for Jericho Bay scallops are indistinguishable from the data presented here 35 years later. Naidu (1969, 1975) monitored growth in a northern, shallow water population of *P. magellanicus* and reported H-infinity values for three locations ranging from 140 to 161 and k values for the same areas ranging from 0.19 to 0.27. These are in close agreement with those reported here for shallow water (Table 3). Posgay and Merrill (1979) reported height-at-age data for scallop samples collected by the National Marine Fisheries Service from Georges Bank and the mid-Atlantic region during the period 1958-1965. Their values for scallops collected along the Maine coast ranged from 40 mm at the second ring to approximately 143 mm at the ninth ring. Again, this compares favorably with our reported values of 39.3 and 140 mm for the second and ninth rings respectively. In a more recent study, Serchuk *et al.* (1982) presented data for scallops from the Gulf of Maine, Georges Bank and the mid-Atlantic bight. These authors showed that the scallops collected from a range of depths in the Gulf of Maine had a smaller mean size-at-age than those from Georges Bank or the mid-Atlantic bight during the first seven years.

MacDonald (1984) and MacDonald and Thompson (1985), in more recent studies of *Placopecten magellanicus*, summarized the existing information on growth in this species and compared growth at three depths in two areas off Newfoundland, Canada as well as off St. Andrews, New Brunswick, Canada and off New Jersey, U. S. A. with collaborative data from various depths in three other locations off Newfoundland. They showed that growth varied with depth at all but one location, that growth was variable between locations, and that growth differences could be attributed to measured differences in food and temperature.

Naidu (1975) found a latitudinal shift in the rate of growth such that the environment in the more northerly locations produced larger maximum-size scallops with a slower growth rate than their more southerly counterparts. MacDonald and Thompson (1985), however, found no such latitudinal differences in growth rate, nor did Serchuk *et al.* (1982). While MacDonald and Thompson (1985) demonstrated slower growth rates in deep water locations than in shallow water areas at their two sampling locations in Newfoundland, they found no differences in the Bay of Fundy near St. Andrews. The differences in growth rates recorded between sampling areas were attributed to variations in environmental parameters. It seems most likely that environmental variables such as temperature, depth and most importantly, food availability, account for the observed differences in scallop growth rates. Choinard (1984) reported the lowest growth rates to date for *Placopecten magellanicus* and attributed these slow rates to the extreme water temperature regime of the Northumberland Strait. Jamieson (1979) also reported low growth rates although not as low as Choinard for a different region of the Northumberland Straight, Central Strait, and also attributed his findings to the wide range of water temperatures in the area. Von Bertalanffy parameters for the sea scallop reported in the literature are summarized by location, author and date in Table 4.

Table 4. Parameters of the von Bertalanffy growth equation ($H_t = H\infty (1 - e^{-k(t-t_o)})$ for the sea scallop, *Placopecten magellanicus*.

$H\infty$	k	t_o	r^2	Location	Source
				Newfoundland, Canada	
				Port-au-Port Bay	Naidu, 1975
152	0.21	−0.48		Boswarlos	
161	0.19	−0.88		West Bay	
140	0.27	0.11		Fox Is. River	
				Sunnyside	MacDonald and Thompson, 1985
176.5	0.19	0.55	0.97	10 m	
165.5	0.20	0.63	0.97	20 m	
158.4	0.16	0.10	0.97	31 m	
				Dildo	MacDonald and Thompson, 1985
174.5	0.19	0.66	0.97	10 m	
168.2	0.19	0.37	0.96	20 m	
147.8	0.22	0.74	0.97	31 m	
				Terre Nova N.P.	MacDonald and Thompson, 1985
163.1	0.24	1.26	0.90	10 m	
151.1	0.22	0.37	0.94	20 m	
146.0	0.17	−0.88	0.92	31 m	
				Colinet	MacDonald and Thompson, 1985
158.6	0.18	0.54	0.96	6 m	
160.1	0.19	0.72	0.96	16 m	
				Northumberland St., P.E.I., Canada	
				Tormantine Bed	Choinard, 1984
103.76	0.37	0.6734		July	
108.83	0.326	0.4636		November	
114.8	0.276	−0.276		Central Strait	Jamieson, 1979
				Bay of Fundy, N.B., Canada	
				St. Andrews	MacDonald and Thompson, 1985
166.9	0.21	0.51	0.96	10 m	
166.0	0.21	0.53	0.98	31 m	
170.2	0.19	0.20	0.97	76 m	
174.3	0.22	−1.238		Gulf of Maine, U.S.A.	Serchuk *et al.*, 1982
				Georges Bank, U.S.A.	
148.9	0.26	1.0		Georges Bank	Posgay, 1962
145.5	0.38	1.5		Georges Bank	Brown *et al.*, 1972
146.4	0.35	1.4		Georges Bank	Posgay, 1976
143.6	0.37	1.0		Georges Bank	Posgay, 1979
152.5	0.34	−1.454		Georges Bank	Serchuk *et al.*, 1982
161.38	0.178	1.195		Georges Bank	Roddick and Mohn, 1985
146.5	0.30	1.32		Northeast Peak	Posgay, 1959
141.8	0.28	1.0		Northern Edge	Posgay, 1959
151.8	0.30	−1.126		Mid-Atlantic Bight, U.S.A.	Serchuk *et al.*, 1982

The effects of environmental variables on growth rate in scallops have most recently been demonstrated by MacDonald and Thompson (1985). They showed, quite convincingly, that the growth rates were directly related to a combination of temperature and food availability with low temperature and low food levels producing the smallest and slowest growing scallops. Posgay (1979) showed a decrease in mean size at age with depth at Eastern Georges Bank. Over four depth ranges from 55 m to 100 m, Posgay showed a decrease in mean size at the fifth ring from 119 mm to 94 mm. Caddy *et al.* (1970) however, did not show significant differences with depth over the five depth ranges from 55 to 144 m in the Bay of Fundy. The mean size of scallops at the fifth ring in their study showed no significant differences between samples. Since these two studies represent different sample sites, it is likely that the differences in growth rates can again be attributed to environmental differences. It is interesting to note here that the Bay of Fundy scallops in both studies, Caddy *et al.* (1970) and MacDonald and Thompson (1985), were the animals that showed no differential growth with depth probably due to hydrographic homogeneity created by strong tidal mixing.

Studies are currently underway to assess the available food rations for the two populations being studied here. It would appear that the reported slow growth rates and smaller size-at-age for the deep-water scallops are primarily due to a lack of suitable food items (Shumway *et al.,* 1987).

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GENETIC POLYMORPHISM IN GASTROPODS: A COMPARISON OF METHODS AND HABITAT SCALES

KENNETH M. BROWN
AND
TERRY D. RICHARDSON
DEPARTMENT OF ZOOLOGY AND PHYSIOLOGY
LOUISIANA STATE UNIVERSITY
BATON ROUGE, LOUISIANA 70803, U. S. A.

ABSTRACT

We compare genetic differentiation in gastropods at two habitat scales, using two methodologies. For the pond pulmonate, *Lymnaea elodes* (Say), we present data on the degree of genetic variance for life histories by comparing variation in traits among full sib groups reared in a common field environment, for two source populations (one vernal, one permanent pond). For the same two populations, as well as a third in another vernal pond, we also present data on allozyme polymorphism. Finally, we contrast genic polymorphism occurring over a much broader habitat scale, using published literature on allozyme polymorphism found respectively in terrestrial, freshwater, and marine environments, and for snails having selfing, outcrossing, or parthenogenetic mating systems.

We found more genetic variation for life history traits in *Lymnaea elodes* occurring in a vernal pond, as variation among sib groups was significant for 5 out of 6 traits measured, versus only 2 out of 6 in a population from a permanent pond. We thus found that unpredictable habitats can favor greater levels of genetic variation in life histories. In contrast, genic polymorphism was similar in all three ponds, with from 27 to 33% of loci polymorphic, and mean heterozygosity ranging only from 8 to 10%. Genetic similarity was high for the two vernal ponds and lower for the more distant permanent pond. Divergence in heterozygosity did occur across broader habitat categories, with lower mean heterozygosity for snails in terrestrial habitats, and self-fertilizers in particular possessing significantly lower heterozygosity within this habitat. The literature survey also indicated more work on allozyme variation is needed in particular for freshwater pulmonates, and we suggest such work along with further work on variation in polygenic characters like life histories.

Although many studies have looked at variation in bioenergetics, life histories, and shell structure among populations of freshwater snails (see reviews in Russell-Hunter, 1978; Russell-Hunter and Buckley, 1983; and McMahon, 1983), little is known of the genetic basis of variation among or within populations for these traits (Brown, 1983). In contrast, quite a bit is known, from studies of allozyme variation, about levels of genic polymorphism in freshwater as well as marine snails (see reviews in Clarke *et al.*, 1978; Berger, 1983; Nevo *et al.*, 1983; Selander and Ochman, 1983). No studies have as yet attempted to study both the genetic basis for variation in life histories and genic polymorphism among and within the same populations of a species. We present such data on variation among sib groups of snails for a number of life history patterns, contrasting them among two populations of the pond snail *Lymnaea elodes* (Say). One population is from a vernal, the other a permanent pond in northern Indiana. For these same two populations, as well as a second vernal pond, we also present data on allozyme variation. To determine if trends in mean heterozygosity appear at a broader habitat scale than between populations, we also review the available literature on allozyme variation in freshwater, marine, and terrestrial gastropods. Within each of these broad habitat categories, we further divide populations as to their breeding systems, including selfing, outcrossing, and parthenogenetic reproduction to determine whether these reproductive modes have any broad effect on polymorphism.

For *Lymnaea elodes*, several studies have concentrated on proximal factors affecting population dynamics, including density dependence (Eisenberg, 1970), habitat productivity and permanence (Hunter, 1975; Brown *et al.*, 1985), and water temperature (Brown, 1979). Brown (1985) used transfer experiments to show that most variation among populations in life histories was due to habitat productivity.

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However, lack of divergence among populations could also be due to pronounced phenotypic and/or genetic variation within populations. For this reason we decided, using snails from both populations, to rear offspring from different sib groups in the same field environment to determine the scale of differences in life histories occurring across sib groups.

We decided to study allozyme polymorphism in the same populations of *Lymnaea elodes* for two reasons. First, genic polymorphism is probably an independent estimator of genetic variation in populations, when compared to genetic variation in phenotypes such as life histories (Lewontin, 1984). Second, little is known of allozyme variation among and within populations of lymnaeid snails or, for that matter, most other freshwater pulmonates. In contrast, allozyme variation has been studied in detail within and among populations of freshwater prosobranchs (Chambers, 1978, 1980; Selander *et al.*, 1978; Dillon and Davis, 1980; Karlin *et al.*, 1980; Selander and Ochman, 1983; Dillon, 1984). Marine gastropods, which are almost exclusively prosobranchs, have also been studied extensively for allozyme polymorphism. Studies have included many species of *Cerithium* (Ritte and Pashton, 1982; Lavie and Nevo, 1986), *Crepidula* (Hoagland, 1985; Woodruff *et al.*, 1986), *Littorina* (Ward and Warwick, 1980), marsh snails such as *Nassarius (Gooch et al.*, 1972), thaidids (Garton, 1984; Garton and Stickle, 1985), and a deep-water species, *Bathybembix bairdii* (Dall) (Siebenaller, 1978).

The genetic structure of terrestrial gastropods is perhaps the best known, with studies ranging from slugs (Foltz *et al.*, 1982a, b, 1984) to a large number on shelled species such as *Cerion, Cepaea,* and *Partula* (see references listed in appendix). We have done the first survey to look explicitly for differences in polymorphism among gastropods across broad habitat categories, although several reviews have considered the effect of mating systems on heterozygosity (Selander and Kaufman, 1975; Nevo *et al.*, 1983; Selander and Ochman, 1983).

METHODS

THE SPECIES AND HABITATS

Lymnaea elodes is a common algivore in temporary ponds and marshes in the northern tier of states in the United States as well as Canada (Brown, 1979). Its life cycle length, fecundity, and shell growth are determined for the most part by habitat productivity and adult snail density (Eisenberg, 1970; Hunter, 1975; Brown, 1985). Adults reproduce in late spring and early summer, and juveniles and some adults estivate over late summer (if the pond dries) and winter (Brown *et al.*, 1985). *Lymnaea elodes* can be eliminated from more permanent habitats (e.g. lakes) by fish predators (Brown and DeVries, 1985). Snails for this study were collected from a vernal pond (Pond A, Brown, 1982) and a more permanent pond (Pond F, Brown, 1982) for experiments assessing variation among sib groups. The vernal pond usually dries by early July and the more permanent pond has water at least until August, after oviposition has been completed. Snails were also collected from a second vernal pond (Pond B, Brown, 1982) for the electrophoretic analyses. This pond usually dries in late July. The three ponds also differ in food levels, with the permanent pond having the greatest periphyton productivity (Brown *et al.*, 1985). All ponds are located in Noble County, Indiana within 30 km of Crooked Lake Biological Station, 33 km NW of Fort Wayne.

VARIATION AMONG SIB GROUPS

The permanent pond was selected as a common rearing site for both populations since higher food levels would not limit egg production (Brown *et al.*, 1985) and snails would be able to complete their life cycles before pond drying. Thirty juveniles were collected from the temporary pond and twenty-five juveniles from the permanent pond in early spring 1981. These snails were placed singly in flow-through containers in Pond F and reared through their entire life cycle. They were paired with a snail from the same source pond for a two week interval when they were between 12 mm and 14 mm shell length to allow outcrossing (lymnaeid snails, like other pulmonates, are hermaphroditic). Companion snails were removed before experimental snails reached 16 mm, the smallest recorded shell length at maturity in these populations (Brown *et al.*, 1985), so that egg laying would not be confounded between the two individuals. Since *Lymnaea elodes* outcrosses preferentially (Brown, 1979), we have assumed snails did not self-fertilize. At weekly intervals, we measured snails and removed all egg cases. Eggs and hatched juveniles were kept over winter in 6*l* aquaria at 13ºC in the laboratory to retard growth and maturation. In spring 1982, we placed an average of 3.5 full sib offspring per temporary pond parent, and 3.0 full sib offspring for each permanent pond parent back in the permanent pond. The same rearing methods were used for offspring as for their parents in the preceding season. A more detailed account of the rearing methods is given in Brown *et al.* (1985).

Six life history traits were measured for each offspring: (1) shell length at maturity; (2) relative age at maturity (days since start of experiment); (3) clutch size (average number of eggs per mass); (4) total fecundity; (5) shell length at death; (6) relative age at death (days since start of the experiment). Exact ages at maturity and death were impossible to determine, as offspring were not separated in the laboratory by date laid. The impact of differing growth rates of offspring over winter in the laboratory was minimized by using initial shell length as a covariate in an analysis of covariance (ANCOVA) that assessed differences among sib groups in each of the life history patterns.

ALLOZYME VARIATION

Approximately 150 snails were collected from each pond and were frozen at −60ºC until analysis when the foot was ground in a chilled cell mill with 0.5 ml of deionized water. Supernatant was absorbed onto wicks of Whatman #3 filter paper and inserted into horizontal starch gels and subjected to electrophoresis for 3-5 hours at 35-55 mA and 200 volts. Gels were stained for the following enzyme systems: (1) acid phosphatase (ACP); (2) esterases (EST); (3) aspartate aminotransferase (AAT); (4) glucose phosphate isomerase (GPI); (5) hexanol dehydrogenase (HEX); (6) leucine aminopeptidase (LAP); (7) malate dehydrogenase (MDH); (8) mannose-6-phosphate isomerase (MPI); (9) 6-phosphogluconate dehydrogenase (PGD); (10) sorbitol dehydrogenase (SDH); (11) superoxide dismutase (SOD). All loci were examined for all populations. Formulas for gel and electrode buffers, as well as stains for these enzyme systems were taken from Shaw and Prasad (1970), Selander *et al.* (1971), Chambers (1980), and Dillon and Davis (1980). Enzymes with multiple loci were numbered by mobility (1=fastest).

Allelic and genotypic frequences were calculated using the BIOSYS-1 FORTRAN program (Swofford and Selander, 1981) which also calculated the percentage of loci polymorphic (using the criterion that a second allele must have a frequency ≥5%). Mean observed and expected heterozygosities (over all loci) for each population and genetic distance indices between populations were also calculated. BIOSYS-1 uses the methods of both Rogers and Nei to calculate genetic distance.

In the literature survey, we either used reported heterozygosities, or calculated heterozygosity over all loci (including monomorphic loci as 0% heterozygous) if raw data on allelic or genotypic frequencies were reported. Each population was then catalogued by habitat and reported mating system. If we could not determine from the paper whether the gastropod was a selfer, outcrosser, or parthenogen, it was placed in the facultative selfing category along with species reported as having a mixed breeding strategy. Data were arc-sine transformed and subjected to ANOVA. The ideal design would be factorial, allowing us to look at the interactive effects of habitats and breeding systems. Due to empty cells, we were constrained, however, to perform two separate one way analyses. First we performed a oneway ANOVA over habitat categories. Second, we performed a oneway ANOVA over breeding systems within each habitat category. Duncan's *a posteriori* multiple range tests were used to compare means (at the 0.05 significance level) if the F statistic was significant.

RESULTS

VARIATION AMONG SIB GROUPS

For sib groups from the permanent pond, the covariate (initial shell length) had significant effects on four of the six life history traits (Table 1). In contrast, only two life history traits, shell length at maturity and clutch size, showed significant variation among sib groups. Variation among sib groups in life history traits was much more obvious in the temporary pond, with significant effects occurring for five of the six traits (Table 2). Initial shell length, however, still had significant effects on the same five traits. Thus, the ANCOVA suggests greater levels of genetic variation for life histories in the vernal pond population, when snails are reared in a common field environment. However, the inital size of individuals when introduced to containers also has substantial effects on life history variation.

Table 1. Analysis of Covariance, with initial shell length as the covariate, of six life history traits among sib groups from a permanent pond. Values are F statistics. One asterik indicates significance at the 0.05 level, two at the 0.01 level.

	SOURCES OF VARIATION			
Traits	Treatments	Covariate	Among Sib Groups	Within Sib Groups
Degrees Freedom	24	1	23	60
Age at Maturity	1.3	6.6*	<1	
Shell length at Maturity	2.9**	28.3**	1.8*	
Clutch Size	3.0**	6.8*	2.9**	
Total Fecundity	1.3	3.1	1.2	
Age at Death	1.7*	6.2*	1.5	
Shell Length at Death	<1	<1	<1	

Table 2. Analysis of Covariance, with initial shell length as the covariate, for six life history traits among sib groups from a temporary pond. Values are F statistics. One asterisk indicates significance at the 0.05 level, two at the 0.01 level.

	SOURCES OF VARIATION			
Traits	Treatments	Covariate	Among Sib Groups	Within Sib Groups
Degrees Freedom	30	1	29	81
Age at Maturity	6.2**	60.7**	4.3**	
Shell length at Maturity	3.6**	43.7**	2.3**	
Clutch Size	3.1**	9.2**	2.9**	
Total Fecundity	2.8**	24.2**	2.1**	
Age at Death	<1	<1	<1	
Shell Length at Death	2.4**	14.0**	2.0**	

ALLOZYME POLYMORPHISM

Patterns in allozyme polymorphisms were consistent across ponds. In all three populations, nine loci were monomorphic: ACP; EST-1; EST-4; GPI; HEX; MPI; PGD; SDH; SOD. In the snails from the first temporary pond (A), 26.7% of the loci were polymorphic, including EST-3, AAT, LAP-1 and MDH. In the second temporary pond, the LAP-2 locus was also polymorphic, with one-third of the loci polymorphic overall (Table 3). In the permanent pond, 26.7% of the loci were polymorphic, namely EST-2, EST-3, LAP-1, and MDH (Table 3).

Mean observed heterozygosity was also similar in each

Table 3. Allelic frequencies, mean expected and observed heterozygosities, and proportion of total loci polymorphic for three pond populations of *Lymnaea elodes*. N refers to number of individuals.

Locus	Allele	Temporary Pond	Second Temporary Pond	Permanent Pond
EST-2	A	0.99	1.0	0.32
	B	0.01	0.0	0.68
EST-3	A	0.07	0.01	0.19
	B	0.03	0.32	0.39
	C	0.90	0.67	0.42
AAT	A	0.85	0.63	1.0
	B	0.15	0.37	0.0
LAP-1	A	0.55	0.01	0.02
	B	0.32	0.35	0.29
	C	0.13	0.64	0.69
LAP-2	A	0.99	0.95	0.99
	B	0.01	0.05	0.01
MDH	A	0.72	0.56	0.94
	B	0.28	0.44	0.06
Mean Observed Heterozygosity (SE)		0.08(0.04)	0.10(0.04)	0.09(0.04)
Mean Expected Heterozygosity (SE)		0.10(0.05)	0.13(0.06)	0.11(0.06)
Percent of Loci Polymorphic		26.7	33.3	26.7
N		150	150	150

Table 4. Pairwise estimates of genetic distance among populations of the pond snail *Lymnaea elodes*. Nei's "unbiased" indices are above the main diagonal, Rogers' indices below.

	Temporary Pond	Second Temporary Pond	Permanent Pond
Temporary Pond	0.0	0.03	0.07
Second Temporary Pond	0.08	0.0	0.06
Permanent Pond	0.14	0.12	0.0

of the populations and ranged from 8 to 10% (Table 3). Mean expected heterozygosities calculated by BIOSYS-1 ranged from 10 to 13%, indicating some degree of heterozygote deficiency in all three ponds as is common in most molluscs. All pair-wise comparisons of the three populations show levels of genetic distance near 0.05 (Table 4), a level characteristic of populations within the same species (Avise, 1976). Both distance indices indicated snails from the permanent pond to be more dissimilar from each of the 2 temporary ponds than the 2 temporary ponds were from each other. This could be due to lower levels of gene flow, since the permanent pond is over 40 km from either of the temporary ponds, which are separated by only 2 km.

Although percent of polymorphic loci and mean observed heterozygosities were similar, there were some interesting differences in allele frequencies among the 3 populations (Table 3). The 2 temporary ponds had similar allele frequencies at EST-2 with allele A being most common. However, in the permanent pond population allele B predominated with a frequency of 0.68. For EST-3, allele C was most common in the temporary pond A population, but dropped to 67% in the second temporary pond population. In the permanent pond, allele A was more common than in ponds A or B. AAT had similar allelic frequencies in both temporary pond populations with allele A declining from 0.85 to 0.63 in the second temporary pond. The pond F population was monomorphic at this locus. Ponds B and F were similar in allelic frequencies at LAP-1 locus with allele C predominating. In contrast, in the pond A population allele A was most common. LAP-2 did not differ much in allelic frequencies among the 3 populations, although with the ≥5% criterion LAP-2 was polymorphic only in the pond B population. MDH differed somewhat in allelic frequencies among the 3 populations although allele A was always more common.

LITERATURE SURVEY

Genic polymorphism has been much more extensively studied in terrestrial gastropods, with over twice as many populations represented than either of the other two habitat categories (Table 5). Outcrossing appeared the most common mating system in each habitat, and populations with obligate selfing were found only in terrestrial snails. Parthenogenetic populations have been studied only in freshwater snails (Table 5). The actual populations and heterozygosities used in the analysis are given in the appendix.

Table 5. Overall mean heterozygosity for habitats and mating systems. Means are weighted for sample size. Numbers in parentheses are sample size.

Mating System	Terrestrial	Freshwater	Marine
Selfers	0.0 (6)	—	—
Outcrossers	0.089 (34)	0.106 (14)	0.173 (13)
Parthenogens	—	0.207 (6)	—
Facultative Selfers	0.047 (10)	0.088 (1)	0.090 (2)
Overall mean	0.061 (50)	0.131 (21)	0.161 (15)

Mean observed heterozygosity was highly significantly different among habitat types ($F_{2,83} = 7.8$; $p < 0.001$). The *a posteriori* test revealed that only terrestrial populations had significantly lower average heterozygosity. Although average heterozygosity can be lowest in terrestrial snails simply because they alone possess selfing populations with no genic polymorphism (Table 5), there appears also to be a general trend, as terrestrial snails in both the outcrossing and facultative selfing categories had the lowest observed heterozygosity of the three habitats. Within terrestrial gastropods, there was, as might be expected, a highly significant difference in mean heterozygosity among mating systems ($F_{2,47} = 16.6$, $P < 0.0001$), and Duncan's multiple range test indicated selfers had a significantly lower average heterozygosity. As also might be expected, outcrossing gastropods had the highest average heterozygosity, and partial selfers had intermediate heterozygosities. In both freshwater and marine habitats there were no significant differences among mating systems in average heterozygosity ($P > 0.05$). Finally, this study of polymorphism in *Lymnaea elodes* reveals levels of heterozygosity just below the average for outcrossing freshwater snails as a group (Table 5), indicating the most probable mating system in these pond populations is mixed.

DISCUSSION

The results of the full sib analyses indicate greater levels of genetic variation for life history traits in snails drawn from a vernal pond population. Perhaps the more unpredictable nature of this habitat has favored the maintenance of genetic variation in life history traits. For example, the vernal pond has extremely unpredictable drying dates from year to year (Brown *et al.,* 1985). In wet years, juvenile recruitment is good, and adult densities are high enough the next year to depress fecundity by density dependence. In years with little rainfall, the vernal pond dries so early that juvenile and adult mortality are intense (Brown *et al.,* 1985). If genetic variation in life histories provides a range of age at reproduction, etc., then at least some individuals would successfully reproduce regardless of the drying date, and genetic variance for life history traits would be maintained. Interestingly, populations of pill clams in vernal ponds in Ohio also have more genetic variation than populations in permanent ponds (McCleod *et al.,* 1981; Burky, 1983). In addition, initial size of individuals introduced to containers also affected life history variation; as initial size increases so does clutch size, age at maturity, shell length at maturity, and age at death (Brown *et al.,* 1985).

In contrast, the electrophoretic data indicate little difference in polymorphism between any of the populations of *Lymnaea elodes.* Levels of polymorphism are very similar in both of the vernal ponds, and essentially the same set of loci vary in the permanent pond as well. Thus, interpretations on levels of genetic variation within and among populations based on the electrophoretic data do not agree with those based on variation among full sibs in life history traits. However, as Lewontin (1984) points out, when there is no known functional relationship between the allozymes and quantitative traits chosen (as in this case), there is no reason to expect a pattern to emerge when comparing the two between populations. Even if a functional relationship exists between the allozymes and quantitative traits, the relative lack of statistical power associated with gene frequency analyses would require a prohibitively large sample size to detect differences at the same level of statistical significance as the quantitative traits. The allozyme polymorphism data do indicate, however, little genetic differentiation among populations, similar to earlier transplant studies (Brown, 1985) suggesting little genetic divergence among populations in life histories. Compared to the average for all populations reported in the literature, mean heterozygosity in these populations of *L. elodes* is very near the value for outcrossing terrestrial pulmonates, slightly less than the average for outcrossing freshwater snails (again mostly dioecious prosobranchs) and much less than dioecious prosobranch marine snails. Therefore, these populations of *L. elodes* probably have a mixed breeding system, with some inbreeding occurring, if for no other reason than the fact that populations go through bottlenecks when ponds dry early (Brown *et al.,* 1985). Also, previous studies of mollusc populations indicate GPI, MPI, PGD, SOD, and HEX are virtually always polymorphic (Clarke *et al.,* 1978; Selander and Ochman, 1983). Interestingly, these loci were monomorphic in these 3 populations of *L. elodes,* possibly due to the recurrent bottlenecks.

However, the literature survey indicated there were differences in heterozygosity over broader habitat categories than these pond populations of *Lymnaea elodes.* Terrestrial pulmonates, regardless of the mating system, have the lowest heterozygosities. This could be due to the nature of their habitats. Terrestrial micro-environments hospitable to snails (the proper temperature and humidity, etc.) might be expected to be more patchily distributed than those in aquatic or marine habitats (Russell-Hunter, 1983). Furthermore, terrestrial snails are relatively immobile and might self-fertilize more than most have considered. Effective population sizes could therefore be low and inbreeding might occur, lowering levels of polymorphism (but for an exception see discussion in Cain, 1983). One would expect that freshwater populations, due to their seasonal nature, could again experience frequent bottlenecks, resulting in lower levels of polymorphism than marine populations where many species also have widely dispersed, planktonic larvae. Indeed, mean heterozygosity in freshwater populations was intermediate to terrestrial and marine values. In each of the habitats, outcrossers had the highest and facultative selfers or selfers the lowest heterozygosity, as would be expected. However, since many authors originally classified populations as selfers only because of low heterozygosity, these results could be somewhat circular. Freshwater parthenogens, interestingly, had the highest average heterozygosity. This suggests the existence of apomictic clones within these populations, as is also seen in parthenogenetically reproducing water fleas (Lynch, 1984) or brine shrimp (Browne *et al.,* 1984).

However, the interpretation of the literature survey was confounded by a number of gaps in the data available on genic polymorphism in gastropods. For example, is selfing a common reproductive mode in other habitats besides terrestrial ones? Although the ability to self might be advantageous in terrestrial habitats because of the patchy nature of the proper microenvironments and consequent low densities of conspecifics, we cannot be certain that predominately selfing populations also occur in either freshwater or marine habitats, but have as of yet not been studied. Similarly, one wonders if parthenogens occur in other habitats besides freshwater. Vail (1978) reports that parthenogenesis is more frequent in upriver viviparid populations, where densities are low and chances of meeting males infrequent. If this is the advantage for parthenogens in freshwater, why have not parthenogens evolved (or more likely been studied) in terrestrial habitats since terrestrial snails are so patchily distributed? Finally, the available data are confounded by taxonomic bias. Most of the terrestrial snails are hermaphroditic pulmonates, capable of self-fertilization, whereas most of the aquatic and marine populations are dioecious prosobranchs.

Overall, this study points to the need for more work on levels of genetic variation in gastropods. We need further studies on the degree of genetic variation in polygenic traits like life histories both among and within populations. Contrasts between temporary and permanent ponds, as well as other important environmental parameters, would also be welcome. Russell-Hunter (1983) suggests the need for incorporation of factors like feeding niche (grazers vs. detritivores), reproductive modes (viviparity vs. oviviparity), possession of planktonic larvae, and colonization ability as well. We also need to fill in the gaps present in studies of allozyme variation, even though existing work is more thorough than studies on variation in polygenic traits. In particular, more work is needed on the degree of allozyme polymorphism among and within populations of freshwater pulmonates. Although we know much about variation in life histories and secondary production among populations of freshwater pulmonates (see reviews in Russell-Hunter, 1978; McMahon, 1983), much less is known of the underlying genetic variation for these traits among and within the same populations.

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Appendix 1. Terrestrial gastropods. Observed heterozygosity and mating system (? or mixed = facultative selfing).

SPECIES	H_O	MATING SYSTEM	STUDY
Milax sowerbyi (Férussac)	0.126	outcross	Foltz *et al.*, 1984
M. budapestensis (Hazay)	0.117	outcross	Foltz *et al.*, 1984
Limax maximus L.	0.027	outcross	Foltz *et al.*, 1984
L. pseudoflavus Evans	0.007	?	Foltz *et al.*, 1984
L. marginatus Müller	0.034	outcross	Foltz *et al.*, 1984
Deroceras caruanae (Pollonera)	0.049	outcross	Foltz *et al.*, 1984
D. reticulatum (Müller)	0.192	outcross	Foltz *et al.*, 1984
Milax gagates (Draparnaud)	0.013	outcross	Noble, unpubl.
Limax tenellus Müller	0.028	outcross	Noble, unpubl.
Deroceras agreste (L.)	0.0	selfer	Noble, unpubl.
Arion ater ater L.	0.0	mixed	Foltz *et al.*, 1982a
A. a. rufus L.	0.059	outcross	Foltz *et al.*, 1982a
A. lusitanicus Mabille	0.082	outcross	Foltz *et al.*, 1982a
A. subfuscus (A) (Draparnaud)	0.062	outcross	Foltz *et al.*, 1982a
A. subfuscus (B)	0.0	mixed	Foltz *et al.*, 1982a
A. circumscriptus Johnston	0.0	selfer	Foltz *et al.*, 1982a
A. silvaticus Lohmander	0.0	selfer	Foltz *et al.*, 1982a
A. hortensis Férussac	0.041	outcross	Foltz *et al.*, 1982a
A. intermedius Normand	0.0	selfer	Foltz *et al.*, 1982a
A. distinctus Mabille	0.186	outcross	Foltz *et al.*, 1982a
A. owenii Férussac	0.044	outcross	Foltz *et al.*, 1982a
Cerion bendalli Pilsbry and Vanatta	0.048	outcross	Woodruff, 1975
Deroceras laeve (Müller)	0.005	mixed	Foltz *et al.*, 1982b
Helix aspera (Müller)	0.200	?	Selander and Kaufman, 1975
Rumina decollata (L.)	0.0	selfer	Selander and Kaufman, 1975
Sphincterochila aharonii (Kobelt)	0.042	?	Nevo *et al.*, 1983
S. cariosa (Oliver)	0.043	outcross	Nevo *et al.*, 1983
S. fimbriata (Bourguignat)	0.104	outcross	Nevo *et al.*, 1983
S. prophetarum (Bourguignat)	0.074	?	Nevo *et al.*, 1983
S. zonata (Bourguignat)	0.079	?	Nevo *et al.*, 1983
Theba pisana (Müller)	0.105	?	Nevo *et al.*, 1981
Partula gibba Bruguiere	0.0	selfer	Johnson *et al.*, 1977
P. mirabilis Crampton	0.167	outcross	Johnson *et al.*, 1977
P. olympia Crampton	0.156	outcross	Johnson *et al.*, 1977
P. otaheitana Férussac	0.175	outcross	Johnson *et al.*, 1977
P. suturalis Pfeiffer	0.167	outcross	Johnson *et al.*, 1977
P. taeniata Mörch	0.134	outcross	Johnson *et al.*, 1977
Achatina fulica Bowdich	0.004	outcross	Selander and Ochman, 1983
Bradybaena similaris Férussac	0.083	outcross	Selander and Ochman, 1983
Cerion incanum (Burch and Kim)	0.051	outcross	Woodruff, 1978
Triodopsis albolabris (Say)	0.100	outcross	McCracken and Brussard, 1980
Xerocrassa seetzeni (Pfeiffer)	0.065	outcross	Nevo, 1978
Cepaea nemoralis (L.)	0.134	outcross	Jones *et al.*, 1980
C. hortensis (Müller)	0.117	outcross	Selander and Ochman, 1983
C. sylvatica (Draparnaud)	0.063	outcross	Selander and Ochman, 1983
Helix pomatia (L.)	0.030	outcross	Jarvinen *et al.*, 1976
Otala lactea Müller	0.196	outcross	Selander and Ochman, 1983
O. vermiculata Müller	0.117	outcross	Selander and Ochman, 1983
Oxychillas cellarius (Müller)	0.198	outcross	Selander and Ochman, 1983
Nymphophilus minckleyi Taylor	0.080	outcross	Selander and Ochman, 1983
Anguispira alternata (Say)	0.148	outcross	Selander and Ochman, 1983

Appendix 2. Freshwater gastropods. Observed heterozygosity and mating system.

SPECIES	H_O	MATING SYSTEM	STUDY
Goniobasis vanhyningiana Goodrich	0.031	outcross	Chambers, 1980
G. floridensis (Reeve)	0.077	outcross	Chambers, 1980
G. dickinsoni Clench and Turner	0.066	outcross	Chambers, 1980
G. athearni Clench and Turner	0.182	outcross	Chambers, 1980
G. albanyensis Lea	0.184	outcross	Chambers, 1980
G. curvicostata (Reeve)	0.078	outcross	Chambers, 1980
Melanoides tuberculata (Müller)	0.306	outcross	Livshits *et al.*, 1984
M. tuberculata (Müller)	0.111	parth	Livshits *et al.*, 1984
Campeloma decisa (Say)	0.095	parth	Selander *et al.*, 1978
C. decisa (Say)	0.033	parth	Selander *et al.*, 1978
Lymnaea elodes	0.088	mixed	This study (all populations)
Biomphilaria straminea (Dunker)	0.082	outcross	Woodruff *et al.*, 1985
B. glabrata (Say)	0.30	outcross	Woodruff *et al.*, 1985
B. havanensis (Pfeiffer)	0.091	outcross	Woodruff *et al.*, 1985
B. alexandria (Ehrenberg)	0.068	outcross	Woodruff *et al.*, 1985
Campeloma geniculum (Conrad)	0.250	parth	Karlin *et al.*, 1980
C. parthenum Vail	0.375	parth	Karlin *et al.*, 1980
Potamopyrgus jenkinsi Smith	0.138	parth	Selander and Ochman, 1983
Viviparous contectoides (Binney)	0.112	outcross	Selander and Ochman, 1983
Physa heterostropha (Say)	0.171	outcross	Selander and Ochman, 1983
Helisoma trivolvis Say	0.136	outcross	Selander and Ochman, 1983

Appendix 3. Marine gastropods. Observed heterozygosity and mating system.

SPECIES	H_O	MATING SYSTEM	STUDY
Adalaria proxima (Alder and Hancock)	0.082	outcross	Havenhand *et al.*, 1986
Onchidoris muricata (Müller)	0.059	outcross	Havenhand *et al.*, 1986
Thais haemastoma L.	0.106	outcross	Garton, 1984
T. lamellosa (Gmelin)	0.017	outcross	Garton and Stickle, 1985
Cerithium scabridum Philippi	0.168	?	Lavie and Nevo, 1986
C. rupestre (Risso)	0.035	?	Lavie and Nevo, 1986
Crepidula onyx Sowerby	0.161	outcross	Woodruff *et al.*, 1986
C. adunca Sowerby	0.052	outcross	Woodruff *et al.*, 1986
C. fornicata (L.)	0.045	outcross	Hoagland, 1985
Austrocochlea constricta Fisher	0.168	outcross	Mulley, 1981
Bathybembix bairdii (Dall)	0.162	outcross	Siebenaller, 1978
Cerithium scabridum	0.620	outcross	Ritte and Pashtan, 1982
C. caeruleum Sowerby	0.635	outcross	Ritte and Pashtan, 1982
Nassarius obsoletus (Say)	0.166	outcross	Gooch *et al.*, 1972
Littorina rudis (Dautzerberg and Fisher)	0.153	outcross	Ward and Warwick, 1980
L. arcana Ellis	0.132	outcross	Ward and Warwick, 1980

THE MUSSELS (MOLLUSCA: BIVALVIA: UNIONIDAE) OF TENNESSEE

LYNN B. STARNES
UNITED STATES FISH AND WILDLIFE SERVICE
UNITED STATES DEPARTMENT OF THE INTERIOR
WASHINGTON, D. C. 20240, U. S. A.
AND
ARTHUR E. BOGAN
DEPARTMENT OF MALACOLOGY
THE ACADEMY OF NATURAL SCIENCES
PHILADELPHIA, PENNSYLVANIA 19103, U. S. A.

ABSTRACT

The unionid fauna that occurs within the political boundaries of the State of Tennessee is reviewed. The fauna reported from the Tennessee, Cumberland, Conasauga and Mississippi river drainages is compared and discussed. There are 155 unionid taxa (species and subspecies) that currently occur or that have been reported historically from the state.

The State of Tennessee, because of the physiographic diversity and discrete drainages encompassed by its boundaries, has one of the most diverse mussel faunas in North America. The state's molluscan fauna is enriched by virtue of having four major river drainages: Mississippi, Tennessee, Cumberland and Conasauga (Coosa River system) (Fig. 1). Bickel (1968) listed 133 unionid taxa from Tennessee but included only the fauna from the Tennessee and Cumberland rivers. A total of 155 taxa have now been recorded from the state. While the unionid fauna from the Tennessee and Cumberland rivers has been historically documented and periodically evaluated, the unionid fauna from the Mississippi River and its direct tributaries in Tennessee, as well as the Conasauga River, has only recently been described.

The vast majority of the unionid fauna is associated with big river habitat. Pollution, channelization, commercial harvest, impoundments and other modifications, have greatly reduced the extent of suitable riverine habitat, curtailing distribution of many species. Of the 24 unionid species listed by the U. S. Fish and Wildlife Service as threatened or endangered, 18 (75%) occur in Tennessee (Hatcher and Ahlstedt, 1982; Bogan and Parmalee, 1983). Most of these species are endemic to the Tennessee and Cumberland rivers (Table 1).

This presentation reviews literature, archaeological and unpublished museum records of the unionid fauna in the State of Tennessee. An in depth analysis of each Tennessee unionid species that involves taxonomy, shell description, distribution and related data is currently under preparation by Dr. Paul W. Parmalee, McClung Museum, University of Tennessee, Knoxville.

RELEVANT FAUNAL STUDIES

Of the four major river drainages, the Tennessee River unionid fauna is the most thoroughly studied. Pilsbry and Rhoads (1897), Coker and Boepple (1912), Ortmann (1918), Brown and Pardue (1980), Pardue (1981) and Dennis (1984) described the unionid fauna in the upper Tennessee River tributaries. Parmalee and Klippel (1984) documented the fauna of the Tellico River, a tributary to the Little Tennessee River. Bogan and Starnes (1983) discussed the Little River unionid fauna. Hickman (1937) surveyed the Clinch River below Norris Dam, prior to the dam's completion. Bates and Dennis (1978) and Ahlstedt (1984) discussed the current status of the unionid fauna of the Clinch River. Dennis (1981) summarized some early historical and certain recent unionid data for the Powell River. Ortmann (1925) described the fauna of the Tennessee River and its tributaries in northern Alabama and southern Tennessee. Isom (1972) reported the freshwater bivalve fauna at the Nickajack Dam Site. Ortmann (1924) described the fauna of the Duck River. Subsequently, van der Schalie (1939, 1973), Isom and Yokley (1968) and Ahlstedt (1981) documented drastic declines in the mussel fauna of the Duck River. The Elk River was surveyed by Remington

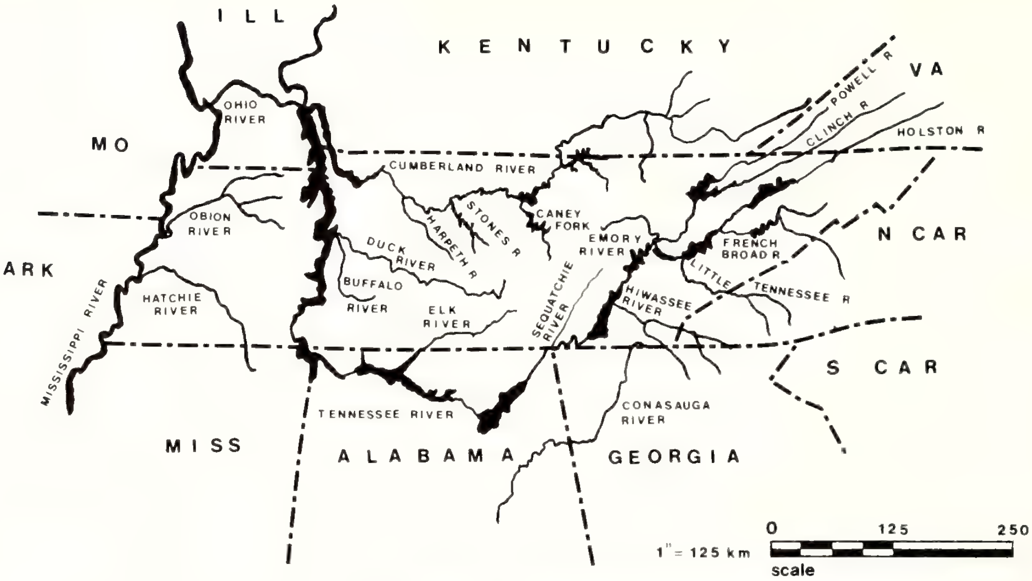

Fig. 1. Map showing the major tributary rivers to the Cumberland, Tennessee and Mississippi rivers in the State of Tennessee.

and Clench (1925), Ortmann (1925), Isom *et al.* (1973) and Ahlstedt (1983). Isom (1969) compared mussel faunas collected in 1965 from the Tennessee River with those recorded prior to impoundment. Scruggs (1960) and Isom and Gooch (1986) made similar pre and post-impoundment comparisons. Yokley (1972) compared the ecology and stocks of species in Kentucky Reservoir. The Tennessee Valley Authority (TVA) Cumberlandian Mollusk Conservation Program, detailed collections from the Clinch, Powell, Nolichucky, Holston, Elk, Duck and Buffalo rivers (Ahlstedt, 1986).

Unionids of the Cumberland River system in Tennessee were studied by Wilson and Clark (1914), Neel and Allen (1964), Isom *et al.* (1979), Parmalee *et al.* (1980), Clarke (1981, 1985), Call and Parmalee (1982), Schmidt (1982), Sickel (1982), Starnes and Bogan (1982) and Stansbery *et al.* (1983). The fauna in the Cumberland River appears similar to that of the Tennessee River, but has not been as thoroughly surveyed and future work could uncover significant differences.

Of the 87 mussel taxa recorded from the Tennessee River, the 69 taxa recorded from the Duck River, and the 78 taxa recorded from the Cumberland River, Ortmann (1924) considered 45 of these to be unique to the Tennessee and Cumberland rivers and referred to them as "Cumberlandian". Ortmann (1925) defined the downriver limits of the Cumberlandian fauna to be Clarksville, Tennessee, on the Cumberland River; Muscle Shoals, Alabama, on the Tennessee River; and between Columbia and Centerville on the Duck River. Below these limits, Interior Basin molluscan species replaced the Cumberlandian species. Ortmann later liberalized these limits, suggesting that some Cumberlandian species had emigrated into the Ohio River as well as into the Interior Basin.

Reports of unionids from the Mississippi River tributaries in Tennessee have been limited to Ortmann (1926a) and van der Schalie and van der Schalie (1950). Recent collections from the Hatchie River (D. Manning, pers. comm.) suggest a diverse fauna. With the exception of the Hatchie River, direct Mississippi River tributaries in Tennessee have suffered extensive channelization resulting in major alterations of their biological communities and a significant reduction of the unionid fauna.

The mussel fauna of the Conasauga River located in the southeast corner of Tennessee is relatively unknown with Hurd (1974), van der Schalie (1981) and museum records providing the only information on this northern Coosa River tributary.

TAXONOMY

Table 1 lists unionid taxa found in the Tennessee and Cumberland rivers in Tennessee. A comparison is made of the nomenclature used by Bickel (1968) and Morrison (1970) with the names used in this paper (Table 1). The American Malacological Union List of Common and Scientific Names [Turgeon *et al.* (in press)] is incorporated as the basis for the taxonomy used in this paper. However, the status of many named subspecific varieties and ecophenotypes has not been resolved. We list them here for clarity. Since the report by Bickel (1968), almost half of the taxa have undergone taxonomic revision. Morrison (1970) and Johnson (1978) declared *Plagiola* Rafinesque, 1819 available over *Dysnomia* Agassiz, 1852, but due to taxonomic questions about the type species, we have chosen to use *Epioblasma* Rafinesque, 1831, the next available generic name. Similarly, the change from *Carunculina* Simpson in Baker, 1898 to *Toxolasma* Rafinesque, 1831 involves five taxa (see Bogan and Parmalee, 1983). Additionally, 12 taxa have been added to the state's total list of species while two, *Fusconaia undata*, (Barnes, 1823) and *Amblema peruviana* (Lamarck, 1819) have been synonymized.

Bickel (1968) used 25 taxa originally described by Rafinesque. Morrison (1970) included 26 nomenclatural changes based on the priority of Rafinesque descriptions. In

Table 1. List of Tennessee unionids found in the Tennessee/Cumberland river systems.

Bickel (1968)	Morrison (1969)	Taxonomy used in this study
Actinonaias carinata (Barnes, 1823)	*Actinonaias ligamentina* (Lamarck, 1819)	*Actinonaias ligamentina*
A. carinata gibba (Simpson, 1900)		*A. ligamentina gibba*
A. pectorosa (Conrad, 1834)		*A. pectorosa*
		Alasmidonta atropurpura (Raf., 1831)
Alasmidonta marginata Say, 1819		*A. marginata*
		A. raveneliana (Lea, 1834)
A. minor (Lea, 1845)	*Alasmidonta viridis* (Rafinesque, 1820)	*A. viridus*
Amblema costata (Rafinesque, 1820)		*Amblema plicata* (Say, 1817)
A. costata perplicata (Conrad, 1841)		*A. plicata perplicata*
A. costata plicata (Say, 1817)		*A. plicata plicata* (Say, 1817)
A. peruviana (Lamarck, 1819)		*A. plicata plicata*
Anodonta grandis Say, 1829		*Anodonta grandis grandis*
		A. grandis corpulenta Cooper, 1834
A. grandis gigantea Lea, 1838		*A. grandis grandis*
A. imbecillis Say, 1829		*A. imbecillis*
A. suborbiculata Say, 1831		*A. suborbiculata*
Anodontoides ferussacianus (Lea, 1834)		*Anodontoides ferussacianus*
Arcidens confragosus (Say, 1829)		*Arcidens confragosus*
Carunculina glans (Lea, 1831)	*Toxolasma livida* Rafinesque, 1831	*Toxolasma lividus glans*
		T. lividus lividus
C. moesta (Lea, 1841)		*T. lividus glans*
C. moesta cylindrella (Lea, 1868)		*T. cylindrella*
C. parva (Barnes, 1823)		*T. parva*
C. texasensis (Lea, 1857)		*T. texasensis*
Conradilla caelata (Conrad, 1834)	*Lemiox rimosus* Rafinesque, 1831	*Lemiox rimosus*
Cumberlandia monodonta (Say, 1829)		*Cumberlandia monodonta*
Cyclonaias tuberculata (Rafinesque, 1820)		*Cyclonaias tuberculata tuberculata*
C. tuberculata granifera (Lea, 1838)		*C. tuberculata granifera*
Cyprogenia irrorata (Lea, 1830)	*Cyprogenia stegaria* (Rafinesque, 1820)	*Cyprogenia stegaria*
Dromus dromas (Lea, 1834)		*Dromus dromas dromas*
D. dromas caperatus (Lea, 1845)		*D. dromas caperatus*
Dysnomia arcaeformis (Lea, 1831)		*Epioblasma arcaeformis*
		E. biemarginata (Lea, 1857)
D. brevidens (Lea, 1831)	*Plagiola interrupta* (Rafinesque, 1820)	*E. brevidens*
D. capsaeformis (Lea, 1834)		*E. capsaeformis*
D. flexuosa (Rafinesque, 1820)		*E. flexuosa*
D. florentina (Lea, 1857)		*E. florentina florentina*
D. florentina walkeri (Wilson and Clark, 1914)		*E. florentina walkeri*
D. haysiana (Lea, 1833)		*E. haysiana*
D. lenior (Lea, 1842)		*E. lenior*
D. lewisi (Walker, 1910)		*E. lewisi*
D. stewardsoni (Lea, 1852)		*E. stewardsoni*
		E. obliquata (Raf., 1820) (=*sulcata* Lea, 1829)
D. torulosa (Rafinesque, 1820)		*E. torulosa*
		E. torulosa cincinnatiensis (Lea, 1840)
D. torulosa gubernaculum (Reeve, 1865)		*E. torulosa gubernaculum*
D. torulosa propinqua (Lea, 1857)		*E. propinqua*
D. triquetra (Rafinesque, 1820)		*E. triquetra*
D. turgida (Lea, 1848)		*E. turgidula*
Elliptio crassidens (Lamarck, 1819)		*Elliptio crassidens*
E. dilatatus (Rafinesque, 1820)		*E. dilatata*
Fusconaia barnesiana barnesiana (Lea, 1838)		*Fusconaia barnesiana*
F. barnesiana bigbyensis (Lea, 1841)		*F. barnesiana bigbyensis*
F. barnesiana tumescens (Lea, 1845)		*F. barnesiana tumescens*
F. cuneolus cuneolus (Lea, 1840)		*F. cuneolus*
F. cuneolus appressa (Lea, 1871)		*F. cuneolus appressa*
F. ebena (Lea, 1831)	*Fusconaia pusilla* (Rafinesque, 1820)	*F. ebena*
F. edgariana (Lea, 1840)		*F. cor cor* (Conrad, 1834)
F. edgariana analoga (Ortmann, 1918)		*F. cor analoga*

Table 1. (continued)

Bickel (1968)	Morrison (1969)	Taxonomy used in this study
F. flava (Rafinesque, 1820)		*F. flava*
F. subrotunda (Lea, 1831)	*F. polita* Say, 1834	*F. subrotunda subrotunda*
F. subrotunda leseuriana (Lea, 1840)	*F. polita lesueriana*	*F. subrotunda lesueriana*
F. subrotunda pilaris (Lea, 1840)	*F. polita pilaris*	*F. subrotunda pilaris*
F. undata (Barnes, 1823)	*F. lateralis* (Rafinesque, 1820)	*F. flava*
Lampsilis anodontoides (Lea, 1831)	*Lampsilis teres* (Rafinesque, 1820)	*Lampilis teres anodontoides*
L. anodontoides fallaciosa (Smith, 1899)		*L. teres teres*
L. fasciola Rafinesque, 1820		*L. fasciola*
L. orbiculata (Hildreth, 1828)	*L. abrupta* Say, 1831	*L. abrupta*
L. ovata (Say, 1817)		*L. ovata*
L. ovata satura (Lea, 1852)		*L. cardium satura*
L. ovata ventricosa (Barnes, 1832)	*L. cardium cardium* (Raf., 1820)	*L. cardium cardium*
		L. siliquoida (Barnes, 1823)
L. virescens (Lea, 1858)		*L. virescens*
Lasmigona complanata (Barnes, 1823)		*Lasmigona complanata*
L. costata (Rafinesque, 1820)		*L. costata*
L. holstonia (Lea, 1838)	*Lasmigona badia* (Rafinesque, 1831)	*L. holstonia*
Lastena lata (Rafinesque, 1820)		*Hemistena lata*
Leptodea fragilis (Rafinesque, 1820)		*Leptodea fragilis*
L. leptodon (Rafinesque, 1820)		*L. leptodon*
Lexingtonia dolabelloides (Lea, 1840)		*Lexingtonia dolabelloides*
L. dolabelloides conradi (Vanatta, 1915)		*L. dolabelloides conradi*
Ligumia recta latissima (Rafinesque, 1820)		*Ligumia recta latissima*
L. subrostrata (Say, 1831)		*L. subrostrata*
Medionidus conradicus (Lea, 1834)		*Medionidus conradicus*
Megalonaias gigantea (Barnes, 1823)	*Megalonaias nervosa* (Rafinesque, 1820)	*Megalonaias nervosa*
Obliquaria reflexa (Rafinesque, 1820)		*Obliquaria reflexa*
Obovaria olivaria (Rafinesque, 1820)		*Obovaria olivaria*
O. retusa (Lamarck, 1819)		*O. retusa*
O. subrotunda (Rafinesque, 1820)		*O. subrotunda*
O. subrotunda lens (Lea, 1831)		*O. subrotunda lens*
O. subrotunda levigata (Rafinesque, 1820)		*O. subrotunda levigata*
Pegias fabula (Lea, 1838)		*Pegias fabula*
Plagiola lineolata (Rafinesque, 1820)		*Ellipsaria lineolata*
Plethobasus cooperianus (Lea, 1834)	*Plethobasus striatus* (Rafinesque, 1820)	*Plethobasus cooperianus*
	P. pachosteus (Raf., 1820)	*P. cicatricosus* (Say, 1829)
P. cyphyus (Rafinesque, 1820)		*P. cyphyus*
P. cyphyus compertus (Frierson, 1911)		*P. cyphyus compertus*
Pleurobema aldrichianum Goodrich, 1931		*Pleurobema aldrichianum*
P. clava (Lamarck, 1819)		*P. clava catillus*
P. coccineum (Conrad, 1836)		*P. coccineum*
P. cordatum (Rafinesque, 1820)	*Pleurobema obliguum* Lamarck, 1819	*P. cordatum*
		P. gibberum
P. oviforme (Conrad, 1834)		*P. oviforme*
P. oviforme argenteum (Lea, 1841)		*P. oviforme argenteum*
P. oviforme holstonense (Lea, 1840)		*P. oviforme holstonense*
P. pyramidatum (Lea, 1831)	*P. obliquata* Rafinesque, 1820	*P. rubrum* (Rafinesque, 1820)
	P. permorsa Rafinesque, 1831	*P. plenum* (Lea, 1840)
Proptera alata (Say, 1817)	*Potamilus alatus*	*Potamilus alatus*
P. laevissima (Lea, 1830)	*P. ohioensis* (Rafinesque, 1820)	*P. ohioensis* (Rafinesque, 1820)
Ptychobranchus fasciolare (Rafinesque, 1820)		*Ptychobranchus fasciolare*
P. subtentum (Say, 1825)		*P. subtentum*
Quadrula cylindrica (Say, 1817)		*Quadrula cylindrica*
Q. cylindrica strigillata (Wright, 1898)		*Q. cylindrica strigillata*
		Q. fragosa (Conrad, 1835)
Q. intermedia (Conrad, 1836)		*Q. intermedia*
Q. metanevra (Rafinesque, 1820)		*Q. metanevra*
		Q. nodulata (Rafinesque, 1820)
Q. pustulosa (Lea, 1831)	*Quadrula bullata* (Rafinesque, 1820)	*Q. pustulosa*
Q. quadrula (Rafinesque, 1820)		*Q. quadrula*
		Q. sparsa (Lea, 1841)

Table 1. (continued)

Bickel (1968)	Morrison (1969)	Taxonomy used in this study
Simpsoniconcha ambigua (Say, 1825)		*Simpsonaias ambigua*
Strophitus rugosus (Swainson, 1822)		*Strophitus undulatus* (Say, 1817)
Tritogonia verrucosa (Rafinesque, 1820)		*Tritogonia verrucosa*
Truncilla donaciformis (Lea, 1828)		*Truncilla donaciformis*
T. truncata Rafinesque, 1820	*Truncilla vermiculata* (Rafinesque, 1820)	*T. truncata*
Uniomerus tetralasmus (Say, 1831)		*Uniomerus tetralasmus*
Villosa fabalis (Lea, 1831)		*Villosa fabalis*
V. lienosa (Conrad, 1834)		*V. lienosa*
V. nebulosa (Conrad, 1834)		*V. iris* (Lea, 1830
V. picta (Lea, 1834)		*V. taeniata picta* (Lea, 1834)
	Villosa teneltus (Rafinesque, 1831)	*V. taeniata punctata* (Lea, 1865)
V. taeniata (Conrad, 1834)		*V. taeniata taeniata*
V. trabalis (Conrad, 1834)		*V. trabalis*
V. trabalis perpurpurea (Lea, 1861)		*V. perpurpurea*
V. vanuxemensis (Lea, 1838)		*V. vanuxemensis*

this analysis, we have included three additional Rafinesque species. Use of taxa originally described by Rafinesque is perceived as controversial due to their convoluted nomenclatural history (Bogan, Williams and Starnes, unpub. data).

FACTORS AFFECTING DISTRIBUTION OF UNIONIDS BY RIVER SYSTEM

MISSISSIPPI RIVER

The nature and size of the Mississippi River along the western border of Tennessee virtually precludes a diverse mollusk fauna. The river elevation annually fluctuates an average of 6 m between winter highs and summer lows. The substratum in shoal areas is sand and gravel while in pools it consists of shifting sand and mud. With few species recorded from the Mississippi River proper, most have come from oxbow lakes or tributary confluences.

Mississippi River tributaries in west Tennessee, with migratory fishes providing the mechanism for dispersal, would be expected to be relatively speciose. Unfortunately, agricultural development of deep soils formed in loess and the resulting deposition of sediments led to channelization of these tributary rivers (Forked Deer, Obion, Wolf and Loosahatchie) prior to documentation of their mussel fauna.

The Hatchie River (Table 2) appears to contain the only extant unionid fauna in Mississippi River tributaries in Tennessee. Due to its relatively uniform sand/silt substratum, diversity is relatively low in the Hatchie River. This limitation of habitat diversity is typical of direct Mississippi River tributaries. Most species recorded in the Hatchie River (D. Manning, pers. comm.) occur in the Tennessee and Cumberland rivers; six species are new to the state list: *Plectomerus dombeyanus* (Valenciennes, 1833), *Uniomerus declivis* (Say, 1831), *Toxolasma texasensis* (Lea, 1857), *Obovaria jacksoniana* (Frierson, 1912), *Potamilus purpurata* (Lamarck, 1819) and *Villosa vibex* (Conrad, 1834). Species such as *Plectomerus dombeyanus* are widespread in Gulf Coast streams.

TENNESSEE RIVER

A total of 126 mussel taxa occur in the Tennessee River and its tributaries. The Tennessee River, encompassing a watershed of over 105,000 km^2, has been divided into upper tributaries (Table 3) and middle and lower tributaries (Table 4).

The French Broad and Holston rivers join to form the Tennessee River. The Clinch and Powell rivers, originating in the Ridge and Valley Province in southwestern Virginia, flow into the Tennessee River. The underlying geology is folded and faulted Paleozoic limestone lying in parallel northeast-southwest ridges. Stream substrata are gravel, rubble and bedrock of primarily limestone (Fenneman, 1938). Water is hard and there are abundant nutrients [USEPA (United States Environmental Protection Agency) STORET Database]. The 45 taxa that Ortmann (1924) considered "Cumberlandian" have been recorded in this physiographic province.

The eastern headwater tributaries of the Tennessee River arise in the Blue Ridge Province. The Watauga, Nolichucky, French Broad, Pigeon, Little, Little Tennessee and Hiwassee rivers originate along the western crest of the Blue Ridge (600-800 m). Except in lower reaches, streams are precipitous with soft water and low amounts of nutrients. Geologically, the area is comprised of metamorphosed sedimentary rocks, gneisses and schists (Fenneman, 1938). Boulders, cobbles and siliceous rocks are typical substrata. While there are endemic fish species such as brook trout [*Salvelinus fontinalis* (Mitchill)] in the Blue Ridge Province, "Cumberlandian" unionid species are rare or totally absent. Molluscan diversity and density, with few exceptions, increases after these streams enter the Ridge and Valley Province, lose gradient and change water chemistry (Bogan and Starnes, 1983).

The Emory River (Table 3), a tributary to the lower Clinch River, is a major stream draining the eastern portion of the Cumberland Plateau. The Emory River crosses geological strata that are characterized by Pennsylvanian sandstone, shale and coal. The substratum is sandy with

Table 2. List of Tennessee unionids found in the Mississippi River tributaries in Tennessee (N = Post 1960; R = Prior to 1960).

Species	North Fork Obion River	Reelfoot Lake	Hatchie River	Loosa-hatchie River	Wolf River	Horn Lake
Amblema plicata	R	R	N	R		
A. plicata plicata	R					
Anodonta grandis		R	N			
A. grandis corpulenta		R	N			
A. imbecillis		R	N			
A. suborbiculata		R	N		R	
Arcidens confragosus	R	R	N			
Elliptio crassidens				R		
Fusconaia ebena	R		N			
F. flava	R		N			
F. flava trigona	R					
Lampsilis cardium satura	R		N			
L. siliquoidea		N				
L. teres teres	R		N	R	R	
L. teres anodontoides			N			
Lasmigona complanata	R		N			
Leptodea fragilis		R	N		R	
Ligumia subrostrata		R	N			
Megalonaias nervosa	R	R	N			
Obovaria jacksoniana			N			
Plectomerus dombeyanus	R	R	N			
Plethobasus cyphus			N			
Pleurobema cordatum			N			
Potamilus ohiensis			N			
P. purpurata			N	R	R	
Quadrula pustulosa		R	N	R		
Q. pustulosa mortoni	R				R	
Q. quadrula	R	R	N	R		
Strophitus undulatus			N			N
Toxolasma parva		R	N			
T. texasensis		R	N			
Tritigonia verrucosa	R		N	R	R	
Truncilla truncata	R	R	N			
Uniomerus declivis			N			
U. tetralasmus			N			
Villosa lienosa			N			
V. vibex			N			
TOTAL TAXA	13	16	32	7	6	1

boulders, bedrock and shale. The water is soft, slightly acidic and nutrient limited. A total of 22 taxa, including 11 Cumberlandian endemics, have been recorded in this drainage, but most occur in the lower reaches when the river enters the Ridge and Valley Province and where the gradient has decreased. The Sequatchie River, a southward flowing tributary of the Tennessee River, drains the Southern Cumberland Plateau. Twenty unionid species are listed from the Sequatchie River (Table 4).

The Highland Rim Province dominates middle Tennessee and encompasses several major tributaries of the Tennessee River. Tributaries draining the crest of the Highland Rim from the south, elevations of 250-300 m, include the Elk, Flint and the Paint Rock rivers (the latter two do not contribute taxa to the Tennessee fauna). The Buffalo River drains the interior of the southwestern Highland Rim while the Duck River drains the eastern and western rim as well as the southern Nashville Basin. These rivers are moderate in gradient, nutrient enriched and have hard water. Substrata consist of loose gravel or chert with limestone bedrock. Typically, these rivers are speciose with the Duck River (Table 4) having 69 taxa; 25 Cumberlandian species inhabit the upper Duck River. The Elk River (Table 4) similarly has 61 taxa recorded from its waters. The Buffalo River (Table 4), a tributary to the Duck River, is problematic; historically 27 taxa have been recorded from this river (van der Schalie, 1973) but few species have been recently collected in the drainage (Ahlstedt, 1986). This is despite the fact that water quality appears acceptable and faunal exchange could have occurred with the Tennessee or Duck rivers since the substratum appears very similar to

Table 3. Mollusks of the Upper Tennessee River and its headwater tributaries (N = Post 1960; R = Prior to 1960; A = Archaeological).

Species	Clinch River	Emory River	Watauga River	French Broad River	Holston River	Little River	Nolichucky River	Powell River	Tenn. River
Actionaias ligamentina	RN				N		N	N	
A. ligamentina gibba	RNA			R	RN		RN	RN	R
A. pectorosa	RN		R		R	R	R	RN	R
Alasmidonta ravenelina					N				
A. marginata	RN		R		RN		N	RN	R
A. viridus	R			R	R	R			
Amblema plicata	RNA	R		R	RN	R	RN	RN	R
Anodonta grandis grandis	N								
A. grandis corpulenta				R					
A. suborbiculata	N								
Cumberlandia monodonta	RN				R	R	RN	R	R
Cyclonaias tuberculata tuberculata	RNA			R	RN		RN	N	R
Cyprogenia stegaria	RNA				R			R	R
Dromus dromas dromas	NA				R			N	R
D. dromas caperatus	R				R			RN	R
Ellipsaria lineolata	R								R
Elliptio crassidens	RNA	R		R	RN		RN	RN	R
E. dilatata	RNA	RN	R	R	RN	N	RN	RN	R
E. dilatata subgibbosus	R								
Epioblasma arcaeformis	RA			R	R				R
E. biemarginata	R				R				
E. brevidens	RN				R			R	R
E. capsaeformis	RNA			R	R	N	RN	RN	R
E. florentina	RA			R					
E. florentina walkeri					R				
E. haysiana	RA				R	R		R	R
E. lenior	R				R				R
E. lewisi	R				R			R	R
E. obliquata	A								
E. propinqua	RA				R				R
E. stewardsoni	RA				R				R
E. torulosa									R
E. torulosa gubernaculum	RNA				R		R	R	
E. triquetra	RNA				R	R	RN	RN	R
E. turgidula	R	R		R	R				
Fusconaia barnesiana	RNA			R	R	RN	N	RN	R
F. barnesiana bigbyensis	RN		R	R	R	R		R	R
F. barnesiana tumescens	R	R		R	R				R
F. cor analoga	R				R			RN	
F. cor	RN							N	R
F. cuneolus appressa	R				R	RN	R		R
F. cuneolus cuneolus	NR	R			R			RN	R
F. subrotunda	RN		R		R		N	RN	
F. subrotunda lesuerianus	RN		R	R			R	R	R
F. subrotunda pilaris	R			R	R				R
Hemistena lata	RN				R			N	R
Lampsilis abrupta	RNA				R				R
L. cardium	R	R		R	R	RN	R	R	
L. fasciola	RNA	R	R	R	RN	RN	N	RN	R
L. ovata	RNA		N		RN		N	RN	R
L. virescens	R	R							
Lasmigona complanata					N				
L. costata	RN	R	R	R	R	N	N	RN	R
L. holstonia	R		R	R	R	R	R	R	R
Lemiox rimosus	RNA				R			RN	R
Leptodea fragilis	RN	N			RN		R	RN	R
L. leptodon	R				R				R
Lexingtonia dolabelloides	RNA			R				N	R

Table 3. (continued)

Species	Clinch River	Emory River	Watauga River	French Broad River	Holston River	Little River	Nolichucky River	Powell River	Tenn. River
L. dolabelloides conradi	R				R				
Ligumia recta	RNA			R	RN		RN	RN	R
L. recta latissima	RN							R	
Medionidus conradicus	RN	R	R		R	RN		RN	R
Obliquaria reflexa	R				R				R
Obovaria retusa	R				R				R
O. subrotunda subrotunda	AR				R				R
O. subrotunda lavigata					R				
Pegias fabula				R	R				
Plethobasus cicatricosus	A				R				
P. cooperianus	RA			R	R				R
P. cyphyus	RNA			R	RN			RN	R
P. cyphyus compertus				R					R
Pleurobema catillus	R				R				
P. clava	A								
P. coccineum	R				R				
P. cordatum	RNA			R	RN		N		R
P. oviforme	RN	R		R	R			RN	R
P. oviforme argenteum	R		R	R	A	RN		R	
P. oviforme holstonse	R	R		R	R				R
P. plenum	RNA			R	R				R
P. rubrum	RNA			R	R				R
Potamilus alatus	RN	N		R	RN		RN	RN	R
Ptychobranchus fasciolare	RNA	RN		R	R		N	RN	R
P. subtentum	RNA				R			RN	R
Quadrula cylindrica cylindrica	RNA				R			RN	R
A. cylindrica strigulata	R				R			R	
Q. intermedia	RA				R		R	N	R
Q. metanevra	RNA				R				R
Q. pustulosa	RNA	N		R	RN		RN	RN	R
Q. sparsa	AN				R			N	
Strophitus undulatus	RN		RN	R	R			RN	R
Toxolasma cylindrellus				R					
T. lividus glans	R	RN				R			
T. lividus lividus	R	R		R	R			R	R
T. parva	R								
Truncilla truncta	RN				R		N		R
Villosa fabalis	R				R		R	R	R
V. iris	RN	R	R	R	R	RN	R	RN	R
V. trabalis	RA								
V. perpurpurea	RN	R			R				
V. vanuxemensis	RNA	R	R	R	R	RN	RN	RN	R
TOTAL TAXA	88	22	15	40	79	20	30	48	63

those rivers.

In addition to geology/water quality apparently affecting mussel diversity and abundance, there is a strong correlation between river drainage size and the occurrence of mussels. In the Tennessee River, the smallest tributary to have a diverse mussel fauna was Copper Creek (in Virginia) with 344.5 km^2 of watershed (Ahlstedt, 1982). Other streams with mussels had over 77.2 km^2 in drainage area.

SUMMARY OF TENNESSEE RIVER

The Tennessee River and its tributaries dominate the state. A total of 126 mussel taxa has been reported from the Tennessee River drainage. This diversity is related to the geology of the area where the headwater tributaries of the river originate. The limestone enriched provinces of the headwater drainages provide an ideal scenario for an expanded mussel fauna: habitat diversity, abundant nutrients and calcium enriched (hard) water. Due to man-induced habitat changes (e.g. pollution and impoundments), the extant fauna in the State is largely restricted to four Tennessee River tributaries (i.e. the Duck, Elk, Clinch and Powell rivers). Construction of the Columbia Reservoir on the Duck River began in 1973 but was essentially halted in 1977. If that impoundment is completed, available habitat for Cumberlandian mussel species will be further restricted by 32-48 km.

CUMBERLAND RIVER

The Cumberland River (Fig. 1) originates in the Cumberland Mountain subprovince of the Cumberland Plateau in southeastern Kentucky. It extends 1,105 km and has a drainage of 48,000 km^2. The Cumberland Plateau is underlain by Pennsylvanian strata consisting of alternating layers of shale, sandstone and coal. Water is soft and low in dissolved nutrients. While the upper Cumberland River is confined to Kentucky, the Big South Fork of the Cumberland River, a major tributary, drains the western Cumberland Plateau in Tennessee. Tributaries to the upper Cumberland River (Little South Fork of the Cumberland, Rockcastle and Laurel rivers) flow through Pennsylvanian-age strata through most of their drainage. The Big South Fork has eroded through Pennsylvanian into Mississippian strata (limestone). Twenty-five unionid species have been recorded from the Big South Fork drainage in Tennessee (Table 5).

As the Cumberland River enters Tennessee from Kentucky it is joined by the Wolf, Obey and Roaring rivers. These drain the eastern Highland Rim and possess substrata and water chemistry similar to the Duck and Buffalo rivers. The Obey River has 30 unionid species while the Roaring River (Table 5) has 7 species.

As the Cumberland River enters the Nashville Basin, it has reduced gradient and meanders westward across the Basin until it re-enters the western Highland Rim. From the south, the Cumberland River receives drainage from the Caney Fork River (southeastern Highland Rim) as well as the Stones River (central Nashville Basin) (Schmidt, 1982). The fauna of the Caney Fork (Table 5) is substantially reduced due to a waterfall below the confluence of the Collins and Rocky rivers. The Caney Fork River has 14 unionid taxa while the Stones River (Table 5) has 49 taxa.

After re-entering the Highland Rim, the Cumberland River flows westward through a deep alluvial floodplain. It receives several major tributaries draining the surrounding Highland Rim including the Harpeth and Red rivers and Yellow Creek (Table 5). These tributaries have upland characteristics with predominately chert-gravel substrata. The Harpeth and Red rivers have 25 and 22 taxa, respectively (Table 5).

SUMMARY OF CUMBERLAND RIVER

A total of 85 mussel taxa has been recorded from the Cumberland River and its tributaries in Tennessee. With 126 taxa recorded from the Tennessee River, this means that numerous taxa including Cumberlandian species *Quadrula sparsa* (Lea, 1841), *Lemiox rimosus* Rafinesque, 1831 and *Lexingtonia dolabelloides* (Lea, 1840) are absent from the Cumberland River. All of the mussel species recorded from the Cumberland River occur in the Tennessee River system.

The cause for this difference in total number of species is probably related to geology. The Cumberland River headwaters are in the nutrient-poor Pennsylvanian strata of the Cumberland Plateau. These tributaries have relatively depauperate faunas. It is only when streams cut through Pennsylvanian strata into limestone that diversity increases (Starnes and Bogan, 1982). A comparison of fauna in the Tennessee and Cumberland rivers reveals that primarily the headwater-mussel species are absent from the Cumberland River. Thus, while these two rivers seem similar physiographically, they are discretely different and this translates into a slightly different mussel fauna.

CONASAUGA RIVER

This tributary to the Coosa River originates in the Blue Ridge Province of northern Georgia and southern Tennessee. The geology of the area is dominated by granite, gneisses, schists and metamorphic rocks (Fenneman, 1938) that produce soft water with low nutrients. Mussels are absent from this headwater area. After the river enters the Coosa Valley (Ridge and Valley) Province, water becomes hard, nutrients increase and bivalves begin to appear. The Conasauga River in Tennessee contains 27 taxa (Table 6). Of these, *Elliptio dilatata* (Rafinesque, 1820), *Anodonta grandis corpulenta* Cooper, 1834, *A. imbecillus* Say, 1829, *Lasmigona holstonia* (Lea, 1838), *Toxolasma parva* (Barnes, 1823), *Medionidus conradicus* (Lea, 1834), *Villosa lienosa* (Conrad, 1834) and *V. vanuxemensis* (Lea, 1838) also occur in the Tennessee/Cumberland rivers and/or their tributaries. The remaining 19 taxa are additions to the state species list and are typical of the Coosa River system and Gulf coast streams (Table 6).

Near the Tennessee/Georgia border unionid species diversity increases. An additional 15 species were collected by Hurd (1974) immediately below that border but have not been collected in Tennessee. These additional species may be limited by habitat diversity or stream size from expanding further upstream in the Conasauga River. Further research into this area could be useful in understanding factors restricting mussel distributions.

DISCUSSION

The earliest unionid faunal descriptions in Tennessee were in the early 1800s. Subsequent malacological work has tended to investigate the same rivers with diverse unionid faunas while ignoring other major streams. It is ironic that no comprehensive faunal surveys have been completed, until recently, on the Conasauga, Hatchie or Mississippi rivers and tributaries in Tennessee. Other works, such as ecological studies of endemic species, are also very limited.

Since Ortmann's work (1918, 1924, 1925) on the Tennessee River system, rivers in this State have undergone considerable change. There are now nine reservoirs on the main Tennessee River, making it essentially a series of impoundments from its origin near Knoxville to its confluence with the Ohio River. While the lack of complete historical data on the early abundance and diversity of molluscan populations in the Tennessee River (Table 6) and its tributaries confounds any efforts to estimate the impact from man-made alterations, changes have taken place. We can neither quantify the change that has occurred in mussel populations during historical times nor can we reliably predict what previous changes portend for the health and survival of existing populations.

Table 4. Mollusks of the Middle and Lower Tennessee River and major tributaries (N = Post 1960; R = Prior to 1960; A = Archaeological).

	Middle Tennessee River				Lower Tennessee River			
Species	Little Tenn. River	Hiwassee River	Sequatchie River	Tenn. River	Elk River	Duck River	Buffalo River	Tenn. River
Actionaias ligamentina				A	NR	RN	RN	
A. ligamentina gibba	NA			RN				RN
A. pectorosa			R		RNA	RN	R	
Alasmidonta marginata	N				R	RN	R	
A. viridus		R	R		R	RN	R	
Amblema plicata	NA		R	RNA	RN	RNA		RN
Anodonta grandis	NA			N	NR	RN		N
A. grandis corpulenta				N				
A. imbecillis						R		RN
A. suborbiculata								N
Arcidens confragosus								N
Cumberlandia monodonta			R					N
Cyclonaias tuberculata	NA		R	RNA	RN	RNA	RN	N
C. tuberculata granifera				N				RN
Cyprogenia stegaria	A			RNA		R		N
Dromus dromas	A			RNA	NR			
Ellipsaria lineolata				RN	NR	R		RN
Elliptio crassidens	NA	R	R	RNA	N	RN		RN
E. dilatata	RNA		R	RNA	RNA	RNA		RN
Epioblasma arcaeformis	A			A				
E. biemarginata			R		R			
E. brevidens	A			A	R	RN		
E. capsaeformis	RA			A	RNA	RNA		
E. flexuosa				A				
E. florentina	R			A	RN	A		
E. florentina walkeri						R	R	
E. haysiana	RA			A	R			
E. lenior						R		
E. lewisi						A		
E. obliquata				A				
E. propinqua	A			A				
E. stewardsoni	A			A				
E. torulosa	A			RA	RN	R		
E. triquetra				A	RN	RNA		
E. turgidula				A	R	R		
Fusconaia barnesiana	RNA	R	R	A	RNA	RNA	RN	
F. barnesiana bigbyensis	R	R			R	R	R	
F. barnesiana tumescens	R	R						
F. cor					RN			
F. cuneolus					RN			
F. cuneolus appressa								
F. ebena				N				RN
F. flava								N
F. subrotunda	RNA			NA	RN			RN
Hemistena lata					RN	R	R	N
Lampsilis abrupta	N			N				RN
L. cardium					R	R	R	R
L. fasciola	RNA		R	RNA	RNA	RNA	R	
L. ovata	RNA			NA	NA	RNA		N
L. teres anodontoides						RN		RN
L. teres teres					N			RN
Lasmigona complanata				N	N	RN	R	
L. costata			R	RA	RN	RN	R	
L. holstonia		R		R		R		
Lemiox rimosus	A			A	RN	RNA		
Leptodea fragilis	N		R	N	RN	RN	RN	N
L. leptodon						R		

Table 4. (continued)

	Middle Tennessee River				Lower Tennessee River			
Species	Little Tenn. River	Hiwassee River	Sequatchie River	Tenn. River	Elk River	Duck River	Buffalo River	Tenn. River
Lexingtonia dolabelloides	NA			RA	RNA	RNA		N
L. dolabelloides conradi						R	R	
Ligumia recta	NA			NA				N
L. recta latissima				N		RN		R
Medionidus conradicus	NA				RNA	RNA		
Megalonaias nervosa				N	RN	RN		RN
Obliquaria reflexa				RN	RN	RN		RN
Obovaria olivaria				N				RN
O. retusa	A			A		R		RN
O. subrotunda	A			A	N	RNA	R	
O. subrotunda lens			R		RN	R	R	
Pegias fabula				RA	RA			
Plethobasus cicatricosus				A				
P. cooperianus	A			RA		N		RN
P. cyphyus	NA			NA				RN
Pleurobema catillus						R		
P. clava			R	A				
P. cordatum	NA			RNA	N	RN		RN
P. oviforme	RNA	R			RNA	RNA	R	
P. oviforme holstonse	R	R		R		R		
P. oviforme argenteum		R			R	R	R	
P. plenum	A			RA				R
P. rubrum	NA			RNA		NR		R
P. coccineum	A							R
Potamilus alatus	NA		R	RNA	N	RN		RN
P. ohioensis	R					N	N	
Ptychobranchus fasciolare	A			RNA	RNA	RN		RN
P. subtentum	A			A	RNA	RA	R	
Quadrula cylindrica	A		R	A	RNA	RNA		
Q. fragosa						R		RN
Q. intermedia				A	RN	RN		
Q. metanevra	NA			RNA	RN			RN
Q. nodulata								N
Q. pustulosa	NA			RNA	N	RN		RN
Q. quadrula					N	RN		RN
Q. sparsa	R			A				
Strophitus undulatus	N			A	RNA	RNA	R	
Toxolasma cylindrellus			RN		R	R	R	
T. lividus glans					N	RN		
T. parva				R				
Tritogonia verrucosa		R		N	RN	RN		RN
Truncilla donaciformis				N	N	RN		RN
T. truncata					N	RN		R
Uniomerus tetralasmus								N
Villosa fabalis					N	RN		
V. iris	R	R	R	R	RN	RNA	RN	
V. taeniata					RNA	RNA	RN	
V. trabalis		R						
V. vanuxemensis		RNA	R	A	RNA	RNA	RN	
TOTAL TAXA	50	12	20	66	61	68	27	45

ARCHAEOLOGICAL RECORD

The archaeological record is a valuable resource in documenting the historical unionid fauna of Tennessee and can provide clues to the early historical abundance and distribution of mussel populations. It provides malacologists with a significant supplement to historical mollusk collections. The archaeological record can provide insight into the former unionid fauna of what is now a dead or severely altered river (e.g. van der Schalie and Parmalee, 1960) or the past distribution of species not documented in historic collections (e.g. Parmalee *et al.,* 1980).

Parmalee and Bogan (1986) discuss the late prehistoric bivalve fauna of the lower Clinch River and document an archaeological assemblage richer and more diverse than that reported by Ortmann (1918). The diverse prehistoric fauna of the main channel of the Tennessee River in East Tennessee has been alluded to by Parmalee (1966), Charles (1973) and Bogan and Parmalee (1977). Parmalee *et al.* (1982) document the past unionid diversity of the Tennessee River above Chattanooga, reporting 45 species from a series of archaeological shell middens. They observed a major shift in the species composition from late prehistoric samples to that fauna represented in reaches impounded since the 1940's. For example, the most common species identified in these archaeological samples was *Dromus dromas* (Lea, 1834), an endangered species (see Bogan and Parmalee, 1983) almost extirpated from the main Tennessee River. The relative dominance of *Dromus* in the prehistoric samples from the Chickamauga Reservoir is comparable to those archaeological assemblages from Widow's Creek in northern Alabama (Warren, 1975) and the large samples reported by Morrison (1942) from the Pickwick Landing basin along the middle stretch of Tennessee River in northwestern Alabama. The relative abundance of the rest of the species is comparable within the archaeological samples from the Clinch River, Chickamauga Reservoir and the two Alabama studies. These archaeological assemblages, when compared with the present fauna, point to some major shifts in species assemblages and abundance over the last 180 years. There has been almost complete extirpation of all species of big river *Epioblasma* sp. as well as other taxa such as *Plethobasus cooperianus* (Lea, 1834), *Actinonaias ligamentina* (Lamarck, 1819), *Quadrula intermedia* (Conrad, 1836), *Cyprogenia stegaria* (Rafinesque, 1820), *Obovaria retusa* (Lamarck, 1819) and *Pleurobema clava* (Lamarck, 1819). These species have been replaced by other taxa such as *Ellipsaria lineolata* (Rafinesque, 1820), *Obliquaria reflexa* Rafinesque, 1820, *Tritogonia verrucosa (Rafinesque, 1820), Megalonaias nervosa* (Rafinesque, 1820) and *Anodonta* spp., which were essentially absent from the archaeological record.

The naiad fauna of the Little Tennessee River, a tributary of the Tennessee River in East Tennessee, was surveyed and reported by Tennessee Valley Authority (1972) as having a fauna of about 20 unionid species. Bogan (1982) summarized the late prehistoric and early historic unionid fauna of the Little Tennessee River as reported by Bogan (1978, 1980, 1983), Robison (1978) and Bogan and Bogan (1985), and had consisted of 46 species; an additional 14 species were expected but not found in the archaeological samples. This reconstruction of the early historic fauna compares favorably with other documented historic naiad faunas from the Clinch, Holston and/or Powell rivers (Ortmann, 1918).

Archaeological bivalves recovered from the Eva site on the west bank of the Tennessee River downstream from the mouth of the Duck River document the former occurrence of at least some of the "Cumberlandian" species as far downstream as the mouth of the Duck River. Casey (1986) documented the prehistoric occurrence of two Cumberlandian species [*Epioblasma arcaeformis* (Lea, 1831), *Dromus dromas*] near the mouth of the Tennessee River (River Mile 17.4) and the Cumberland River (River Mile 26) in Kentucky. Parmalee (1982) and Parmalee and Klippel (1986) reported the former occurrence of at least 26 species in the Duck River based on a sample of naiads recovered from early and mid-Holocene deposits. Robison (1986) included a discussion of aborginal unionid samples from the Duck and upper Elk rivers.

Ortmann (1926b), in discussing the unionid fauna of the Green River in Kentucky, noted the absence of *Epioblasma torulosa* (Rafinesque, 1820) from the Cumberland River (excluding a probably spurious record from Walker). However, Parmalee *et al.* (1980) compared the modern fauna of the Cumberland River with archaeological samples and documented the former occurrence of *E. torulosa* in the Cumberland River and noted that it was a common species in the prehistoric faunal assemblage. Casey (1986) recorded specimens of the *E. torulosa* complex from these same sites.

These examples clearly exemplify the importance of archaeological material to the study of prehistoric and early historic unionid distributions. The archaeological record is an important supplement to modern collections and provides a historical perspective on some of the changes in the naiad fauna that have occurred in the past 180 years.

FAUNAL EXCHANGES

Evidence of faunal exchange between the Tennessee and Cumberland rivers and the Ozark Region is supported by archaeological records showing a larger range for "Cumberlandian" species than envisioned by Ortmann. Ortmann (1925) recognized that these two regions shared certain species, but did not elaborate. *Cumberlandia monodonta* (Say, 1829) and *Epioblasma turgidula* (Lea, 1848) are shared exclusively by these two regions. There is additional evidence of faunal affinities with closely related taxa [i.e. *Fusconaia barnesiana* (Lea, 1838) in the Tennessee and Cumberland rivers and *F. ozarkensis* (Call, 1887) in the Ozarks]. Similar affinities exist for *Ptychobranchus fasciolare* (Rafinesque, 1820) and *P. occidentalis* (Conrad, 1836), and *Cyprogenia stegaria* (Rafinesque, 1820) and *C. alberti* (Conrad, 1850). The Tennessee and Cumberland river drainages share many upland fish species groups and subgenera with the Ozarkian region [for example: *Notropis galacturus* (Cope), *N. telescopus* (Cope), *Typhlichthys subterraneus* Girard and *Fundulus catenatus* (Storer) are exclusively shared by these regions (Starnes and Etnier, 1986)]. These two regions exclusively share fish and mussel species and yet these same species are absent from adjacent tributaries to the Mississippi or Ohio rivers.

Thus far, discussions of the Tennessee and Cumberland rivers have indicated that their mussel faunas are very similar. Ortmann (1925) reported 10 taxa that were known to be present in the Tennessee River but absent from the Cumberland River. Of the Cumberlandian species found in the Tennessee and Cumberland rivers, the following are absent from the lower Tennessee (Ortmann, 1924): *Quadrula*

Table 5. Species of the Cumberland River and its tributaries (N = Post 1960; R = Prior to 1960; A = Archaeological).

Species	Cumberland River	Big So. Fork Cumberland River	Obey River	Caney Fork River	Stones River	Harpeth River	Red River	Roaring River
Actinonaias ligamentina	RNA		R		N	R		
A. ligamentina gibba	R			R			R	
A. pectorosa		N	R	R	N		R	
Alasmidonta atropurpurea		N		N				
A. marginata	R		NR				N	
A. viridis					N	N	N	
Amblema plicata	NA		R		RN			
A. plicata perplicata	R						R	
A. plicata plicata	N							
Anodonta grandis	RN				RN			
A. imbecillis	RN				RN			
Anodontoides ferussacianus	R							R
Cumberlandia monodonta	RN			R	N			
Cyclonaias tuberculata	RNA		R		N	R	R	
C. tuberculata granifera	R							
Cyprogenia stegaria	RNA							
Dromus dromas	RNA					R		
Ellipsaria lineolata	RN				N			
Elliptio crassidens	RNA	N	R				R	
E. dilatata	RNA	N	R		N	R	R	
Epioblasma arcaeformis	A				R			
E. brevidens	NA	N		R	N			
E. capsaeformis	RA	?	R	R				
E. flexuosa	A							
E. florentina	RA		R		R	R	R	
E. florentina walkeri	RN		?		RN	R	R	
E. havsiana	RA							
E. lenior					RN			
E. obliquata	N			R		R		
E. stewardsoni	A							
E. torulosa	NA							
E. triquetra	N		R					
Fusconaia ebena	RN							
F. flava	RNA				RN	R		
F. subrotunda	RNA		R					
Hemistena lata	R	R						
Lampsilis abrupta	RNA		R					
L. cardium	R	N			RN	R		
L. fasciola	RA	N	R		RN	R	R	R
L. ovata	RNA	N	R	R	N		R	
L. teres anodontoides	RN		R		N	R	R	
L. teres teres	RN							
Lasmigona complanata	RN			R	RN	R	R	
L. costata	RNA	N	R	R	RN	R	R	R
Leptodea fragilis	RN				N			
Lexingtonia dolabelloides	NA							
Ligumia recta latissima	RNA	N	R		N	R		
Medionidus conradicus		N			RN			R
Megalonaias nervosa	RN				RN		R	
Obliquaria reflexa	RNA		R	R	N			
Obovaria olivaria	RN							
O. retusa	RNA							
O. subrotunda	RA		R		RN	R	RN	
Pegias fabula		N		RN	N			
Plethobasus cicatricosus	A			R				
P. cyphyus	RNA							
P. cooperianus	RNA							
Pleurobema catillus	R							

Table 5. (continued)

Species	Cumberland River	Big So. Fork Cumberland River	Obey River	Caney Fork River	Stones River	Harpeth River	Red River	Roaring River
P. clava	NA							
P. cordatum	RNA				N			
P. gibberum				N				
P. oviforme		N	R		N			
P. plenum	RNA							
P. rubrum	RNA				N			
P. coccineum	NA	N			N			
Potamilus alatus	RNA	N	R		N		R	
P. ohioensis	R					R		
Ptychobranchus fasciolare	RNA	N	R		N		R	
P. subtentum		N	R	R		R		
Quadrula cylindrica	RNA		R		N			
Q. fragosa	RN					R		
Q. metanevra	RNA		R					
Q. pustulosa	RNA	N			N	R		
Q. quadrula	N				N			
Simpsonaias ambigua					N			
Strophitus undulatus	R	N	R		N	R	R	
Toxolasma lividus glans								R
T. lividus lividus					RN	?		
T. parva					N			
Tritogonia verrucosa	RN	N	R		N	R	R	
Truncilla donaciformis	R				N	R		
T. truncata	RN			R	N		R	
Villosa iris	A	N	R		N			
V. lienosa	R				N			
V. taeniata picta						R		R
V. taeniata punctata								R
V. taeniata	RNA	N	R	N	RN			
V. trabalis		N	RN					
V. vanuxemensis					N	?	R	
TOTAL TAXA	68	25	30	14	49	25	22	7

cylindrica strigillata (Wright, 1898); *Plethobasus cyphus compertus* (Frierson, 1911); *Alasmidonta raveneliana* (Lea, 1834); *Villosa perpurpurea* (Lea, 1861); *Epioblasma torulosa gubernaculum* (Reeve, 1865); *E. stewardsoni* (Lea, 1852); *E. lewisi* (Walker, 1910). A total of 87 mussel taxa have been reported from the Cumberland River drainage while 126 taxa have been recorded from the Tennessee River drainage. Thus, while many species are shared, the fauna from the Cumberland River does not include every species present in the Tennessee River.

Faunal similarities occur between the two rivers because of habitat and geological similarities instead of faunal exchanges that would tend to make the faunas identical in at least those rivers/streams where the exchange occurred (see Starnes and Etnier, 1986). There are geological differences between the two river drainages. Among these, there is less physiographic diversity in the Cumberland River drainage with the tributaries originating in Pennsylvanian strata while those of the Tennessee River originate in Ridge and Valley strata. This geologic dissimilarity between the Tennessee and Cumberland tributaries probably contributes to the dissimilarity in the total number of species. The Clinch River, a part of the upper Tennessee River system, has had 89 taxa reported from its drainage. In contrast, the Stones River, the tributary with the most diverse fauna in the Cumberland River system, had only 49 taxa reported.

FAUNAL ALTERATIONS

As stated earlier, man-made river alterations have affected mussel populations throughout recorded history. In impoundments the species *Anodonta grandis* Say, 1829; *A. imbecillis; A. suborbiculata* Say, 1831; *Obliquaria reflexa; Tritogonia verrucosa; Elliptio crassidens* (Lamarck, 1819) and *Quadrula quadrula* (Rafinesque, 1820) have expanded their populations and distribution. While these species have proliferated in reservoirs, those species requiring riverine environments for themselves or for their host fish species have disappeared. Riverine species associated with the lower Tennessee and Cumberland rivers appear least affected by impoundments, perhaps because there is little difference between a deep, slow-flowing river and a deep, slow-flowing impoundment.

Table 6. Mollusks tabulated by river system (N = Post 1960; R = Prior to 1960; A = Archaeological).

Species	Tennessee River Upper	Tennessee River Middle	Tennessee River Lower	Conasauga River	Cumberland River	Mississippi River Tributaries
Actionaias ligamentina	RN	A	RN		RNA	
A. ligamentina gibba	RN	RN	RN		R	
A. pectorosa	RN	R	RN		R	
Alasmidonta atropurpurea					N	
A. marginata	RN		RN		RN	
A. viridus	R	R	RN		N	
Amblema plicata					RNA	RN
A. plicata perplicata					R	
A. plicata plicata	RN	RNA	RN		RNA	RN
Anodonta grandis	RN	N	RN		RN	RN
A. grandis corpulenta	R			N		RN
A. imbecillus			RN	N	RN	RN
A. suborbiculata	N		N			Rn
Anodontoides ferussacianus					R	
Arcidens confragosus			N			RN
Cumberlandia monodonta	RN	R	NR		RN	
Cyclonaias tuberculata	RN	RNA	RN		RNA	
C. tuberculata granifera	N	N	RN		R	
Cyprogenia stegaria	RN	RNA	RN		RNA	
Dromus dromas dromas	RN	RNA	R		RNA	
D. dromas caperatus	R					
Ellipsaria lineolata	R	RN	RN		RN	
Elliptio arctata				N		
E. crassidens	RN	RNA	RN		RNA	R
E. dilatata	RN	RNA	RN	N	RNA	
E. dilatata subgibbosus	R					
Epioblasma arcaeformis	R	A			RA	
E. biemarginata			R			
E. brevidens	RN	A	RN		RNA	
E. capsaeformis	RN	RA	RN		RA	
E. flexuosa		A			A	
E. florentina	R	A	N		RA	
E. florentina walkeri	R		RN			
E. haysiana	R	RA	R		RA	
E. lenior	R		R		N	
E. lewisi	R					
E. metastriata				N		
E. obliquata		A			RN	
E. propinqua	R	A				
E. stewardsoni	R	A			A	
E. torulosa torulosa	R	RA	R		NA	
E. torulosa gubernaculum	RN					
E. triquetra	RN	A	RN		N	
E. turgidula	R	A	RN			
Fusconaia barnesiana barnesiana	RN	RA	RN			
F. barnesiana bigbyensis	RN	R	R			
F. barnesiana tumescens	R	R	R			
F. cor analoga	R					
F. cor cor	RN		N			
F. cuneolus cuneolus			N			
F. cuneolus appressa	R					
F. ebena		N	RN		R	RN
F. flava			N		RN	RN
F. flava trigona						R
F. subrotunda	RN		N		RNA	
F. subrotunda lesuerianus	RN					
F. subrotunda pilaris	RN	RA	RN			

Table 6. (continued)

Species	Tennessee River Upper	 Middle	 Lower	Conasauga River	Cumberland River	Mississippi River Tributaries
Hemistena lata	RN		RN		R	
Lampsilis abrupta	RN	N	RN		RNA	
L. altilis				N		
L. cardium	R	R	R		RN	
L. cardium satura						RN
L. clarkiana				N		
L. fasciola	RN	RNA	RN		RNA	
L. ornata				N		
L. ovata	RN	RNA	RN		RNA	
L. siliquoidea						N
L. straminea claiborensis				N		
L. teres			RN		RN	RN
L. teres anodontoides						N
L. virescens	R					
Lasmigona complanata	RN		RN		RN	RN
L. costata	RN	RA	RN		RNA	
L. holstonia	R	R	R	N		
Lemiox rimosus	RN	A	RN			
Leptodea fragilis	RN	RN	RN		RN	RN
L. leptodon	RN		R			
Lexingtonia dolabelloides	RN	RA	RN		NA	
L. dolabelloides conradi	R		R			
Ligumia recta	RN	NA	N			
L. recta latissima	RN	N	RN		RNA	
L. subrostrata						RN
Medionidus acutissimus				N		
M. conradicus	RN		RN	N	RN	
Megalonaias nervosa		N	RN		RN	RN
Obliquaria reflexa	R	RN	RN		RNA	
Obovaria jacksoniana						N
O. olivaria		N	RN		RN	
O. retusa	R	A	RN		RNA	
O. subrotunda	R	A	RN		RNA	
O. subrotunda levigata	R					
O. subrotunda lens		R	RN			
Pegias fabula	R	R			N	
Plectomerus dombeyanus						RN
Plethobasus cicatricosus		A			RA	
P. cooperianus	R	RA	RN		RNA	
P. cyphyus	RN	NA	RN		RNA	N
P. cyphyus compertus	RN	NA	RN		RNA	N
Pleurobema aldrichianum				N		
P. catillus	R		R		R	
P. clava		RA			NA	
P. cordatum	RN	RNA	RN		RNA	N
P. georgianum				N		
P. gibberum					N	
P. hanleyanum				N		
P. johannis				N		
P. oviforme	RN	R	RN		N	
P. oviforme holstonse	R	R	R			
P. oviforme argenteum	RA		R			
P. perovatum				N		
P. plenum	RN	AN	R		RNA	
P. rubellum				N		
P. rubrum	RN	RA	R		RNA	
P. coccineum	R	R	R		NA	
P. troschelianum				N		

Table 6. (continued)

Species	Tennessee River Upper	Tennessee River Middle	Tennessee River Lower	Conasauga River	Cumberland River	Mississippi River Tributaries
Potamilus alatus	RN	RNA	RN		RNA	
P. ohiensis			RN		N	RN
P. purpurata						RN
Ptychobranchus fasciolare	RN	RNA	RN		RNA	
P. greeni				N		
P. subtentum	RN	A	RN		R	
Quadrula cylindrica	RN	RA	RN		RNA	
Q. cylindrica strigulata	R					
Q. fragosa			RN		RN	
Q. intermedia	RN	A	RN			
Q. metanevra	RN	RNA	RN		RNA	
Q. nodulata			N			
Q. pustulosa	RN	RNA	RN		RNA	RN
Q. pustulosa mortoni						RN
Q. quadrula			RN		N	RN
Q. sparsa	N					
Simpsonaias ambigua					N	
Strophitus connasaugaensis				N		
S. undulatus	RN	A	RN		RN	RN
Toxolasma cylindrellus			R			
T. lividus glans	R		RN	N	R	
T. lividus lividus	R				RN	
T. parva	R	R		N	N	RN
T. texasensis						RN
Tritigonia verrucosa		RN	RN		RN	RN
Truncilla donaciformis		N	RN		RN	
T. truncata	RN		RN		RN	RN
Uniomerus declivis						N
U. tetralasmus						N
Villosa fabalis	R		RN			
V. iris	RNR	RN		N	NA	
V. lienosa				N	RN	N
V. taeniata picta	N?				R	
V. taeniata punctata					R	
V. taeniata taeniata			RN		RNA	
V. trabalis	R	R			R	
V. trabilis perpurpurea	RN					
V. vanuxemensis	RN	R	RNA	N	RN	
V. vanuxemensis umbrans				N		
V. vibex				N		N
TOTAL TAXA	94	73	89	27	85	35

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MORPHOLOGY OF GLOCHIDIA OF *LAMPSILIS HIGGINSI* (BIVALVIA: UNIONIDAE) COMPARED WITH THREE RELATED SPECIES

D. L. WALLER[1], L. E. HOLLAND-BARTELS[1], AND **L. G. MITCHELL[2]**
[1]U. S. FISH AND WILDLIFE SERVICE
NATIONAL FISHERIES RESEARCH CENTER
P. O. BOX 818
LA CROSSE, WISCONSIN 54602-0818, U. S. A.
[2]IOWA STATE UNIVERSITY
DEPARTMENT OF ZOOLOGY
AMES, IOWA 50011, U. S. A.

ABSTRACT

Glochidia of the endangered unionid mussel *Lampsilis higginsi* (Lea) are morphologically similar to those of several other species in the upper Mississippi River. Life history details, such as the timing of reproduction and identity of host fish, can be readily studied if the glochidia of *L. higginsi* can be distinguished from those of related species. We used light and scanning electron microscopy and statistical analyses of three shell measurements, shell length, shell height, and hinge length, to compare the glochidia of *L. higginsi* with those of *L. radiata siliquoidea* (Barnes), *L. ventricosa* (Barnes), and *Ligumia recta* (Lamarck). Glochidia of *L. higginsi* were differentiated by scanning electron microscopy on the basis of a combined examination of the position of the hinge ligament and the width of dorsal ridges, but were indistinguishable by light microscope examination or by statistical analyses of measurements. Analysis of variance and multivariate (principal component) analysis separated *L. radiata siliquoidea* from the other three species by virtue of its larger size, but discriminant function analysis classified only 38% of the glochidia of *L. higginsi* correctly compared with 83% of those of *L. radiata siliquoidea*.

The glochidia of most unionid freshwater mussels are obligate parasites on the gills or fins of fishes. Glochidia discharged from the marsupial gills of females attach and encapsulate on fish and undergo organogenesis to the juvenile stage (Coker *et al.*, 1921). Information on the life history and recruitment of mussel species can be readily developed by the collection and identification of glochidia. For example, Zales and Neves (1982a, b) using light microscopy, determined the timing of glochidial release, periods of infection, and the identity of fish hosts for four lampsiline mussels by collecting and identifying glochidia in stream drift and on fish gills.

Glochidia of the endangered *Lampsilis higginsi* (Lea) are morphologically similar to those of several other species of Lampsilinae in the upper Mississippi River (Surber, 1912, 1915). Before information about the reproductive cycle and host fishes could be determined, a method for operational/field identification of the glochidia of *L. higginsi* was required.

Several methods have been used to study glochidia. Shell shape and gross features have been described by light microscopy (Lefevre and Curtis, 1910; Surber, 1912, 1915; Utterback, 1933; Inaba, 1941), shell dimensions have been measured (Surber, 1912, 1915; Inaba, 1941; Wiles, 1975; Zale and Neves, 1982a), and scanning electron microscopy has been used by several researchers (Heffelfinger, 1969; Calloway and Turner, 1978; Clarke, 1981, 1982; Rand and Wiles, 1982). Although Surber (1912) provided camera lucida drawings and measurements of glochidial length and width from samples of *Lampsilis higginsi*, he provided no definitive identification of the species. No further descriptions of *L. higginsi* glochidia have been reported.

Our objective was to ascertain simple techniques that could be used routinely in the field, including light microscope examination and measurements of shell dimensions, to differentiate the glochidia of *Lampsilis higginsi* from those of three other lampsiline mussels *(L. radiata siliquoidea* (Barnes), *L. ventricosa* (Barnes), and *Ligumia recta* (Lamarck)

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in the upper Mississippi River system. In addition, scanning electron microscopy was used to study aspects of the comparative ultrastructure of the shells of these four species.

MATERIALS AND METHODS

Gravid females of 15 species of mussels, in addition to *Lampsilis higginsi*, were collected from the upper Mississippi River (Pools 7 and 10) by handpicking and brailing. After preliminary examination, we selected *L. radiata siliquoidea* (here termed *L. radiata*), *L. ventricosa*, and *Ligumia recta* for detailed study because of the close similarity of their glochidia to those of *L. higginsi*. We removed glochidia from live females by using a hypodermic needle and syringe to flush the marsupial portion of the gill. Glochidia that were infective and therefore selected for examination responded by snapping their valves shut when placed in a 1.0% NaCl solution. Other glochidia came from females preserved in 10% formalin or 70% ethanol. In measuring length (maximum anterior-posterior), height (maximum dorsal-ventral), and hinge length, we examined 20 glochidia per female under a microscope (100x) fitted with an ocular micrometer.

Data analyses were conducted using the Statistical Analysis System (SAS Institute, 1979) at Iowa State University, Ames. Statistical significance is defined as $P < 0.05$.

Photographs were taken of representative specimens of glochidia of each species for qualitative comparisons of general shell features. All aspects of the shell were photographed, including lateral views showing the shape of the shell and hinge, and the position, size, and shape of adductor muscle, a dorsal view showing the hinge and beak sculpture, and an anterior-posterior view showing the flange and shell gape.

Some glochidia of each species were fixed in 10% buffered formalin and held in 70% ethanol for scanning electron microscopy. Samples were prepared by critical point drying and sputter coating with platinum palladium (Postek *et al.*, 1980). Shells were studied at magnifications of 300x to 10,000x.

RESULTS AND DISCUSSION

STATISTICAL ANALYSIS

One-way analyses of variance revealed that overall significant differences existed among glochidia of the four species in the three morphometric characteristics measured. However, the source of the difference was not due to *Lampsilis higginsi*, but to *L. radiata* which was significantly greater in length, height, and hinge length than the other three species (which did not differ significantly from one another). (Table 1.) In addition, a multivariate (principal component) analysis also did not separate *L. higginsi* from the other species (Fig. 1). The first principal component had similar loadings for all three characteristics (height = 0.59, length = 0.60, hinge length = 0.54) and accounted for 77% of the total variance in the correlation matrix. Component 2 (hinge length = 0.83, height = 0.47, length = 0.29) accounted for only 16% of the variance. Again, *L. radiata* could be separated from the other three species by its larger size, but *L. higginsi* did not differ significantly from *L. ventricosa* and *Ligumia recta*.

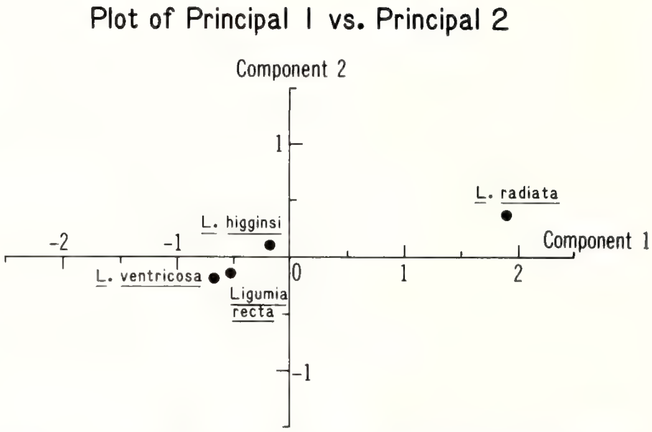


Fig. 1. Principal component analysis. The large size of *Lampsilis radiata* glochidia separates it from the other forms along component 1.

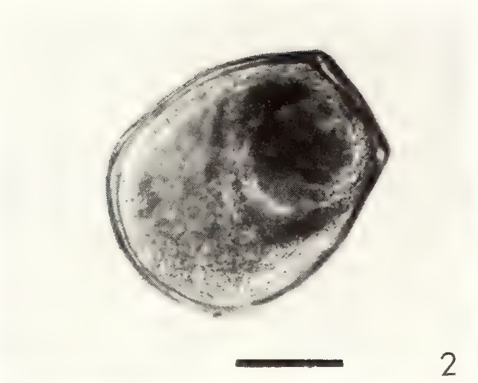
Glochidia of *Lampsilis higginsi* were correctly classified in 39% of the observations by discriminant analysis, but 55% were misclassified as either *L. ventricosa* or *Ligumia recta* (Table 2). Correct classifications were 50% for *L. ventricosa* and 48% for *Ligumia recta*. Discriminant function analysis was the most accurate for glochidia of *L. radiata* correctly classifying 83% of the glochidia, 10% were misclassified as *L. higginsi*.

LIGHT MICROSCOPY

The shape and appearance of shells of the four species examined were so similar that identification by observation with the light microscope was not possible (Fig. 2). Our general observations of the shells were similar to those of Lefevre and Curtis (1910) for hookless glochidia in shape of the shell, the double margin around the periphery of the shell, granulations on the lateral surface, the position and shape of adductor muscle, and the presence of two pairs of microprojections. When profiles of the shells of each species were compared by overlaying transparencies of shells of the same size, no obvious differences in shape could be detected, although about 4% of the glochidia in one female *Ligumia recta* were much higher than most glochidia of this species (height $\bar{x}$ = 296 μm). The relative position of the hinge ligament could be discerned in some glochidia of each species at 40x. The hinge ligament in *L. recta* was centrally located whereas that in the three *Lampsilis* species was more posterior. The position of the adductor muscle was not considered for use in identification because the larval adductor muscle is lost soon after a glochidium attaches to a fish. Other features of the glochidium were not adequately resolved by light microscopy to be useful for species identification.

SCANNING ELECTRON MICROSCOPY

Scanning electron microscopy showed all four species have similar surface features. A series of semi-circular ridges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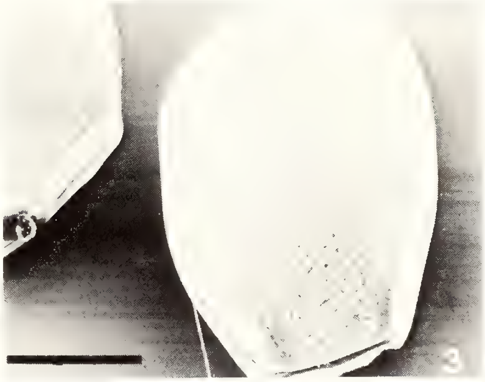
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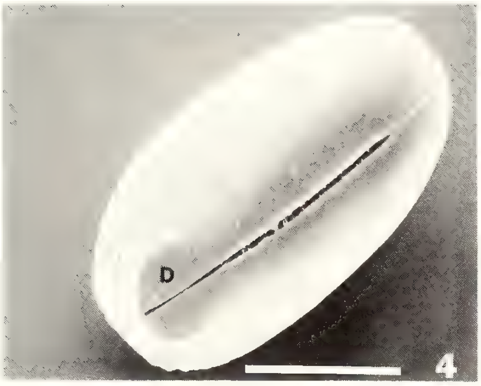

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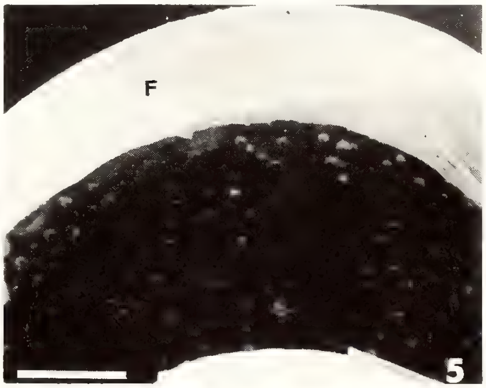

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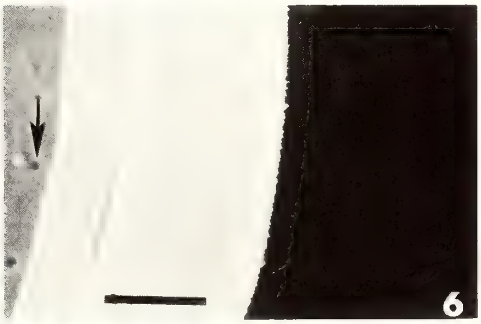
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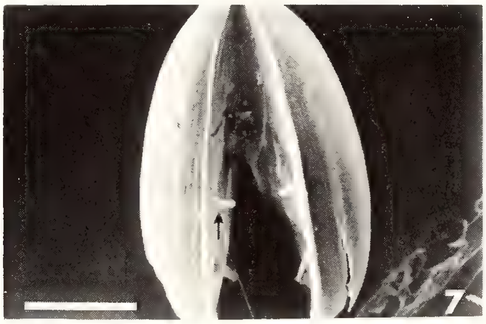
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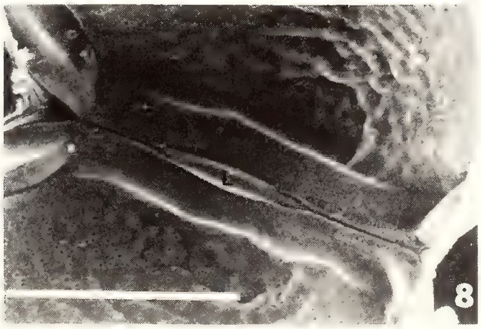

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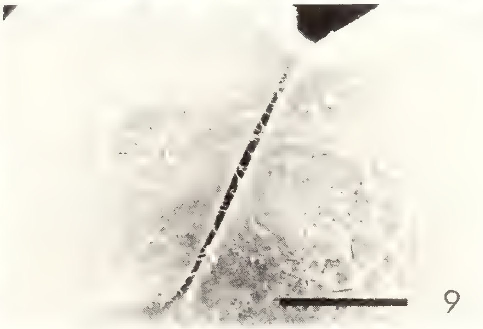
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Fig. 2. Glochidia of *Lampsilis higginsi:* light microscope photograph (scale bar = 100 μm). **Fig. 3.** Scanning electron micrograph of characteristic features of shell valve of Lampsilinae glochidia (scale bar = 100 μm). **Fig. 4.** Scanning electron micrograph (anterior view) showing flattened dorsal ridges (D) of *Lampsilis higginsi* (scale bar = 100 μm). **Fig. 5.** Ventral flange (F) and a portion of the lateral shelf of glochidium of *L. ventricosa* (scale bar = 20 μm). **Fig. 6.** Ventral flange showing fine tooth-like projections and pits on internal surface (arrow) of glochidium of *L. ventricosa* (scale bar = 10 μm). **Fig. 7.** Internal view of the glochidium as seen in the gaping shell: mantle, adductor muscle, and microprojections (arrow) (scale bar = 100 μm). **Fig. 8.** Internal view of hinge ligament, placed slightly posterior in *Lampsilis radiata* (scale bar = 100 μm). **Fig. 9.** External sculpturing of the shell at the dorsal edge in *Lampsilis ventricosa* glochidium (scale bar = 50 μm).

Table 1. Mean measurements (standard deviations in parentheses) of glochidia of four Lampsilinae mussels. Means for each measured characteristic with the same superscript are not significantly different from each other ($P = 0.05$) (Student-Newman-Keul's test of means).

Species	Number of glochidia	Number of females	Measurements (μm)		
			Height	Length	Hinge
Lampsilis higginsi	96	3	259^a (8.0)	215^a (4.2)	110^a (4.2)
L. radiata	220	11	271^b (1.2)	228^b (0.8)	120^b (0.5)
L. ventricosa	556	19	257^a (0.9)	216^a (0.8)	107^a (0.5)
Ligumia recta	180	9	259^a (0.9)	213^a (0.5)	107^a (0.5)

on the lateral surface become wrinkled near the hinge (Fig. 3). In addition, each valve has many pits on both the internal and external surface, which have sometimes been interpreted as pores (Arey, 1924; Zs.-Nagy and Labos, 1969; Calloway and Turner, 1978; Rand and Wiles, 1982). When viewed from the lateral external surface, the shell does not appear to be porous, but in cross-sectional and internal examinations of the valves, the pits appeared to be continuous. This apparent discrepancy could have been explained by Calloway and Turner (1978), who noted that the external surface appeared perforated only at accelerating voltages of 20 kilovolts and greater. They concluded that the periostracum was not perforated and that the appearance of pores on the outer surface was an artifact of the scanning electron microscope. Perhaps electrons penetrate the periostracum at 20 kilovolts making it appear transparent and the pits appear as pores. Posterior and anterior edges of each valve are flattened near the dorsal aspect, forming a smooth surface about 65 μm long (dorso-ventral) and 25-40 μm wide (medial-lateral) here referred to as dorsal ridges (Fig. 4). The peripheral edges of the valves are turned inward to form a continuous shelf around the inner margin. Ventrally, the shelf forms a flange or lip believed to be analogous to the hook of anodontine mussels described by Lefevre and Curtis (1910) (Fig. 5). The flange is about 13-19 μm wide and extends the width of the ventral shell margin. Fine, tooth-like projections, previously described as microstyles (Clarke, 1985), cover all except the proximal one-third of the flange (Fig. 6). The microstyles decrease in length to micropoints on the inner edge of the flange. In all four species, the microstyles are arranged in irregular vertical rows and about 14-17 rows cover the flange from the inner to the outer edge. The inner shell margin provides an attachment site for the mantle, a thin sheet of tissue covering the inner valve surface except in the region of the adductor muscle. The single adductor muscle was also seen internally near the dorsal margin. A pair of cylindrical microprojections, about 24-26 μm long, previously described as "sensory hairs" (Lefevre and Curtis, 1910), is near the ventral margin of the valve (Fig. 7). At the dorsal edge of the valve, the shelf folds inward forming an articulating surface for junction of the valves. The larval ligament connects the valves at this hinge line (Fig. 8).

Table 2. Summary of percent of each species classified as either *Lampsilis higginsi, L. radiata, L. ventricosa,* or *Ligumia recta* by discriminant analysis.

Known species	Percentage classified into species				
	Lampsilis higginsi	*L. radiata*	*L. ventricosa*	*Ligumia recta*	Number of specimens
Lampsilis higginsi	39	6	22	33	96
L. radiata siliquoidea	10	83	5	2	220
L. ventricosa	19	8	50	24	556
Ligumia recta	20	5	27	48	180

Table 3. Width of the dorsal ridge of the four Lampsilinae species. Mean dorsal ridge widths with the same superscript are not significantly different from each other ($P = 0.05$) (Student-Newman-Keuls' test of means).

Species	N	Width of ridge (μm)		
		Mean	SD	Range
Lampsilis higginsi	9	27.20^a	1.75	25.0-29.2
L. radiata	9	33.48^b	3.13	28.0-37.9
L. ventricosa	10	34.70^b	3.06	30.0-40.0
Ligumia recta	8	28.66^a	0.96	25.8-30.0

We concentrated on three features of the shell in our efforts to distinguish among the species: (1) position of the hinge ligament; (2) width of the flattened dorsal ridges; (3) sculpturing on the lateral shell surface. The first two features proved to be the most useful for separating *Lampsilis higginsi.* Hinge ligaments were central in glochidia of *Ligumia recta*, whereas they were slightly more posterior in *L. higginsi, L. ventricosa,* and *L. radiata.* The dorsal ridges of each valve, measured at their greatest width, differed significantly among species (Table 3). The ridge width was usually narrower in *L. higginsi* and *Ligumia recta* (250-300 μm) than in *L. ventricosa* and *L. radiata* (280-400 μm).

The shell sculpture showed no major differences among the species, though there was some subtle variation. We attempted to identify photographs of each species on the basis of shell sculpture alone, but could not consistently detect a representative pattern on each shell.

CONCLUSION

The objective of this study was to find an operational/field method for routine identification of *Lampsilis higginsi.* Light microscopy and statistical analyses of shell dimensions were found to be inadequate for species differentiation. Scanning electron microscopy can be used to differentiate glochidia of *L. higginsi* from the other three species on the basis of the position of the hinge ligament and the width of the dorsal ridges, but the technique is expensive and impractical for identification of small samples of glochidia collected in the field. The technique could be of use when there is justification for a significant investment of time and expense in identification of glochidia. Hoggarth and Cummings (pers. comm.) used scanning electron microscopy to identify glochidia of *Anodonta grandis grandis* Say on fish in field collections and suggested this technique was more labor efficient than artificial infection experiments for determining host fishes. On the contrary, we have found that artificial infection requires much less equipment, training, and expense than scanning electron microscopy and is more practical for routine use.

Laboratory culture of glochidia and juveniles (Isom and Hudson, 1982; Hudson and Isom, 1984) could be another route for developing early life histories. Investigators could follow the growth of a mussel and document developmental stages at which *Lampsilis higginsi* can be positively differentiated from related species by light microscopy. One could then verify fish hosts by holding field-collected fish in the laboratory until juvenile mussels have dropped off and developed into an identifiable stage. Recruitment of a species could also be evaluated by identification of juveniles in the field.

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RESEARCH NOTE

A TECHNIQUE FOR TRAPPING SANDFLAT OCTOPUSES

JANET R. VOIGHT
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
UNIVERSITY OF ARIZONA
TUCSON, ARIZONA 85721, U. S. A.

ABSTRACT

An intertidal population of *Octopus digueti* Perrier and Rochebrune was sampled without apparent sex or size bias (except for the smallest size classes) by placing artificial shelters in the intertidal zone. Comparisons of captures between the octopuses' natural shelters, large gastropod shells, and the artificial shelters, glass bottles, revealed no differences in the sex or size of the octopuses captured. The bottle trap technique is an inexpensive means of sampling *O. digueti.* The technique provides large numbers of untraumatized octopuses and can define the local species distribution in this potentially shelter-limited population.

A basic problem in the study of octopus populations is that of reliable sampling. Most workers have employed hand capture by divers armed with chemical irritants (*e. g.* Smale and Buchan, 1981; Ambrose, 1984; Hartwick *et al.*, 1984; Aronson, 1986), or capture by trawls (Mangold and Boletzky, 1973; Hatanaka, 1979; Guerra, 1981; Boyle and Knobloch, 1982; Boyle, 1986). Both techniques have inherent drawbacks. Divers locate more large animals than small ones, and are limited by water clarity, depth restrictions, past experiences of individual divers, the type of shelter available to the octopuses and the persistence of den middens (Ambrose, 1983; Hartwick, 1983; Van Heukelem, 1983). Trawl captures are limited to species occurring on trawlable bottoms, and are biased by net mesh size and varying trawl times (Boyle, 1983).

Beginning in ancient times, a number of widely separated fishing cultures have captured octopuses by placing artificial shelters in the sea and recovering them after the octopuses have taken up residence. Such trapping techniques have been successful for *Octopus dofleini* (Wülker) in the northeast Pacific, *O. briareus* Robson in the Caribbean, *O. tetricus* Gould in Australia and *O. vulgaris* Cuvier in the Mediterranean (Lane, 1957; Roper *et al.*, 1984).

Current uses of traps in the study of octopuses have been limited to providing a few untraumatized octopuses for laboratory studies (Nixon, 1969; Joll, 1976, 1977) and to assessing the fisheries potential of a population (Whitaker and DeLancey, 1986). Although octopuses use a wide variety of shelters in the wild, selection experiments have revealed that octopuses show an aversion to transparent shelter in both laboratory (Mather, 1982) and field (Aronson, 1986) studies. Shelters with narrow apertures are preferred by *Octopus joubini* Robson (Mather, 1982).

This paper describes a trapping technique that has proven useful in the study of *Octopus digueti* Perrier and Rochebrune, a small (generally less than 40 g) octopus occurring on sandy bottoms throughout the Gulf of California. This species typically uses the shelter provided by vacant gastropod and bivalve shells (Hochberg, 1980) that can be limiting, since individuals are often found under shell fragments, in bottles or cans, or even buried in the sediment (Perrier and Rochebrune, 1894; pers. obs.). This technique uses brown glass bottles as artificial shelters that serve as inexpensive and reliable traps. They provide a means of sampling the population and can provide relatively untraumatized octopuses for laboratory studies.

MATERIALS AND METHODS

The study area was located in Choya Bay, Sonora, Mexico. The bay is a 5 km^2 area of sandflats, located about 5 km northwest of the town of Puerto Peñasco, in the northern Gulf of California. Extreme vertical tidal ranges (to 7 m) and the gentle slope of the bottom made intertidal trapping feasible. *Octopus digueti* is common in Choya Bay, especially in areas of permanent water cover such as tide pools or channels where shell refuges are abundant.

Bottle traps used in this study were barrel-shaped, 325 ml brown glass beer bottles (Cerveza Corona) that taper

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to a 17 mm neck diameter. A nylon electrician's cable tie secured around the bottle neck and a metal paper clip slipped through the cable tie fastened each trap to an anchor line and facilitated easy removal. Shells of *Muricanthus nigritus* Philippi and *Hexaplex erythrostomus* Swainson with apertures ranging from 29x42 mm to 76x98 mm were used as controls for the bottle traps, both for estimating capture rates, and for sampling larger octopuses that do not utilize bottle traps. The shells were assembled into trap lines using the same method as the bottle traps, with a cable tie inserted through two holes drilled in the outer whorl of each shell.

Traplines consisted of 10 traps attached to loops tied at one meter intervals on 40 or 50 pound test (18 or 23 kg) nylon monofilament. Each line was staked at both ends by a 0.3 m length of steel reinforcing bar driven into the substratum. Three lines of shell traps and nine lines of bottle traps were set between 10 July and 24 Sept 1984. Most traplines were staked in optimal habitat for the octopuses, areas with abundant shell debris and with water during the lowest tides. To determine the vertical distribution of the species in the intertidal zone, lines were staked from −1.3 to +0.7 m. Both the outer flat habitat, an area with coarse sand and abundant shell debris, and the inner flat habitat, an area of fine sediment and few shells (Flessa and Ekdale, 1987), were sampled by bottle traps.

All traplines were left staked in the intertidal zone throughout the duration of the study. They were checked at 24 hour intervals during spring tides when low tides were at −0.6 m or lower. The number of traps containing octopuses, and the number of traps lost were recorded at each inspection.

Traps with resident octopuses were removed from the line and replaced with empty traps. Captured octopuses were taken in their traps to the marine laboratory at the Centro de Estudios de Desiertos y Oceanos (CEDO) near Puerto Peñasco and placed in aquaria. Each individual was induced to leave its trap by draining the water. All octopuses were narcotized by a brief immersion in a 3-4% ethanol-seawater solution. Body weight was determined on a triple beam balance, after water was drained from the mantle. A variety of measurements were also made on each individual, of which head width is reported here. The hyaline cranium (Boyle *et al.*, 1986) is the most rigid part of the octopus body and, as such, could be indicative of size selection imposed by the narrow neck of the bottle-traps. The sex of each individual over 15.0 g was determined by the presence in males of a hectocotylized third right arm, and by its absence in females. Octopuses under 15.0 g were considered to be juveniles. The octopuses were returned to within 800 m of the trap locality at the next suitable low tide.

RESULTS

Of 2,244 total traps set overnight for twenty-one nights, 317 captured octopuses, for an overall capture rate of 14.1%. Traplines placed in optimal octopus habitats in the outerflats routinely contained octopuses. However, traplines in the innerflats never captured any octopuses. Captures were rare where the outer and innerflats intergraded. In optimal habitats, shell traps were statistically more effective than were bottle traps (18.3% versus 11.7%, $\chi^2=6.85$, $p<.01$). Trap losses from breakage and dislodgement over the three month period were 18.8% for the shell traps and 26.7% for the bottle traps.

Table 1. Sexual composition of *Octopus digueti* sampled by bottle traps and shell traps. Individuals weighing less than 15 g were considered juveniles and were excluded from this analysis. Chi-square for deviation from 1:1 sex ratio for bottle trap sample $\chi^2=2.66$, $p>0.05$; for shell trap sample $\chi^2=.38$, $p>0.05$.

	Bottle Traps	Shell Traps
Males	88	23
Females	111	19
Juveniles	55	2

Potential competitors for shelter in the bottle traps were not seen. However, juvenile spotted sand bass (*Paralabrax maculatofasciatus* Steindachner) occasionally took refuge in the shell traps and could have excluded the octopuses.

Sex ratios of adult *Octopus digueti* captured by both types of trap were not significantly different from 50:50 (chi-square analysis with a Yates correction factor, Table 1). Head widths of animals captured by bottle traps were not significantly different from those captured by shell traps ($p>0.10$, Kolmogorov-Smirnov Two-sample Test), although the bottle traps captured more small individuals (Table 2).

The mortality observed in this study was limited to two animals that died as a result of wedging themselves into bottle necks. Otherwise, captured octopuses survived the trip to the laboratory and the narcotization.

Table 2. Number of head widths of individual *Octopus digueti* from bottle traps and shell traps.

Head width in mm	Bottle traps	Shell traps
10.0-11.9	1	1
12.0-13.9	14	0
14.0-15.9	34	0
16.0-17.9	49	5
18.0-19.9	72	10
20.0-21.9	69	18
22.0-23.9	14	10
24.0-25.9	1	0

DISCUSSION

Bottle traps provided an inexpensive, reliable means of collecting large numbers of *Octopus digueti.* The total capture rate (14.1%) compares favorably with capture rates obtained by snap-trapping small mammals (Voight and Glenn-Lewin, 1979), although during a one-year study of this *O. digueti* population, total capture rates were strongly affected by seawater temperatures (Voight, unpub. data). Whitaker and DeLancy (1986) reported a 26% capture rate in a potting study of *O. vulgaris* sampled at intervals of from several days to several weeks along the Atlantic coast of North America. In their study, as in this one, octopuses collected in traps were spared injuries associated with trawl captures and the exposure to chemicals required for hand collection by divers, hence they were relatively untraumatized.

The comparison of capture rate between shells and bottles showed that shells were more effective as traps and less likely to be lost. However, bottles had an advantage in that they were more easily acquired than were large numbers of suitable gastropod shells, and they had narrow apertures. In the laboratory, *Octopus joubini*, a small sandflat octopus from the Gulf of Mexico and the Caribbean, prefer shelters with relatively narrow apertures to those with wide apertures (Mather, 1982). A similar preference in *O. digueti* could explain the attractiveness of the narrow-necked bottles with sloping sides as shelter. The funnel-shaped upper third of the bottle allowed small individuals to contact a solid wall, if they remained near the bottle neck. The barrel shape allowed large individuals, once past the narrow aperture, ample space while maintaining contact with the solid wall. Thus, the shape of the bottle assured little size bias.

The aversion to shelters that allow light penetration, reported in *Octopus joubini* and *O. briareus* (Mather, 1982; Aronson, 1986), could have been minimized in this study by the use of brown glass. This aversion, if present in *O. digueti*, could have reduced the capture rate of the bottle traps.

Very small individuals, less than 18 mm head width, were underrepresented by both techniques. Since *Octopus digueti* produces young in the study area that immediately assume a benthic existence (Hanlon and Forsythe, 1985), it is assumed that all sizes of octopuses were available for trapping. Young octopuses are likely to be more secretive and less mobile than are adults, which may explain their lower capture rate.

No sex bias was apparent in *Octopus digueti* with either trap technique in the present study (Table 1), the sexes are thought to be equally represented in other *Octopus* populations (Wells and Wells, 1977; Guerra, 1981; Smale and Buchan, 1981; Aronson, 1986). The strongly female biased sex ratios that have been observed in *O. dofleini* have been attributed to behavioral differences between the sexes (Hartwick *et al.*, 1984). Field studies of *Eledone cirrhosa* (Lamarck) also show a female biased sex ratio, which has been attributed to female migration into shallow waters (Boyle, 1983).

In addition to monitoring the population, the bottle trap technique effectively demonstrated the local species distribution. The capture rate of octopuses declined to zero with the change in substratum from coarse sand and shells to fine sand with few shells. Without the trap technique, extensive surveys would have been required to define the upper limit of the species' range in the intertidal zone.

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RESEARCH NOTE

THE NEED FOR QUANTITATIVE SAMPLING TO CHARACTERIZE SIZE DEMOGRAPHY AND DENSITY OF FRESHWATER MUSSEL COMMUNITIES

ANDREW C. MILLER AND **BARRY S. PAYNE**
U. S. ARMY ENGINEER
WATERWAYS EXPERIMENT STATION
ENVIRONMENTAL LABORATORY
VICKSBURG, MISSISSIPPI 39180-0631, U. S. A.

ABSTRACT

An accurate estimate of density of all mussels in a community, regardless of size, requires collecting total substratum samples. As part of a monitoring program on bivalves in large rivers, 0.25 m^2 quadrat total substratum samples were collected by divers at two dense beds, one in the upper Mississippi River at Prairie du Chien, Wisconsin, the other in the lower Ohio River near Olmsted, Illinois. A linear relationship existed between the cumulative number of species obtained and the logarithm of the number of quadrats sampled. Using this relationship it was estimated that 40 and 200 samples, respectively, were required to accurately assess species richness at high and low density sites in the upper Mississippi River. Because of the contagious nature of these beds, reliable density estimates for all unionid species required at least 7 to 12 quantitative samples. Dominant species were characterized by infrequent but fairly strong recent recruitment, illustrating the necessity of collecting and processing total substratum samples to obtain juveniles.

An evaluation of the condition of a mussel bed should be based upon measurements of species richness, relative abundance, density, and recruitment. Accurate determination of all of these parameters, except perhaps species richness, requires that quantitative samples of bottom material be obtained and sieved for all live mussels regardless of size. Although this approach is used in most benthic surveys, it is rarely applied in studies of mussels in large rivers. In these habitats mussels often occur in substratum too consolidated to allow quantitative sampling using devices such as Ponar, Eckman, Peterson, or Shipek dredges (Isom and Gooch, 1986). The Surber sampler (Henderson, 1949) and suction pumps (Mattice and Bosworth, 1979) have been used to quantitatively collect bivalves in shallow streams. However, the occurrence of unionids in deep water and in consolidated gravels has made quantitative studies of these communities difficult.

Brails, or crowfoot dredges, were developed by commercial fishermen and have been used to study the distribution and relative abundance of unionids in large rivers (e.g. Smith, 1898; Baker, 1903; Coker, 1918; Starret, 1971), but surveys conducted with these devices suffer numerous and variable biases (e.g. Scruggs, 1960; Krumholz *et al.*, 1970; Thiel *et al.*, 1980; Kovalak *et al.*, 1986). Semi-quantitative surveys have been performed by having divers equipped with SCUBA retrieve mussels by feeling for them within quadrats (e.g. Duncan and Thiel, 1983; Isom and Gooch, 1986; Kovalak *et al.*, 1986) or along transects (e.g. Brice and Lewis, 1979; Isom and Gooch, 1986). Search and feel methods are almost certainly biased against species characterized by small-sized animals or juveniles of species characterized by large-sized animals, but have improved our understanding of mussel distribution in large rivers relative to use of brails (e.g. Isom and Gooch, 1986; Kovalak *et al.*, 1986).

The purpose of this paper is to describe a sampling approach that utilizes quantitative substratum removal to accurately assess size demography and density of unionids in large river habitats. These studies were conducted as part of a monitoring program on population and community structure of bivalves at prominent beds to assess impacts of water resource development.

STUDY SITES

Studies were conducted at two mussel beds, one

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located in the east channel of the upper Mississippi River near Prairie du Chien, Wisconsin (RM 636) and the other in the lower Ohio River near Olmstead, Illinois (RM 967). Both beds were several km long, at least 300 m wide, and were found in stable substratum. Sampling sites were in fairly deep water (4-6 m at typical low water levels in early fall), and located a minimum of 100 m from the periphery of the bed. Mussel beds were identified from published information (e.g. Havlik and Stansbery, 1978, for the site on the upper Mississippi River and Williams, 1969, for the site on the lower Ohio River). The approximate size of each bed, and location of sites was determined by a diver performing a general reconnaissance. A mussel bed was defined as a contiguous area of stable substratum where densities were at least 10 individuals per m^2.

In the east channel of the Mississippi River in October 1984, 10 samples were taken at each of five sites that were separated by about 1 km. In July 1985, 30 samples were taken at each of two sites that consisted of three subsites (see Hurlbert, 1984) sampled 10 times each. Preliminary sampling at these and other beds indicated that at least ten samples would be required to estimate species richness and total mussel density. Study sites were separated by a distance of 0.5 to 1.5 km; subsites were within 50 m of each other. In addition, a pair of quadrats were taken every 1.2 m along a 14.4 m transect in a dense part of the bed.

At the mussel bed in the Ohio River, four sites that were about 50 m apart were sampled six times in September 1983. In October 1985 a single site was sampled 13 times, and in September 1986, eight sites were sampled eight times and one site was sampled four times. The 1983 and 1985 surveys were conducted in the upstream half of the bed; the 1986 survey was conducted near the downstream limit of the bed.

METHODS

At each site in a bed, a diver collected samples from within an aluminum 0.25 m^2 quadrat that was positioned in a haphazard manner near an identifying buoy. The diver transferred all substratum, which included sand, gravel, shells, and live organisms, from each quadrat into a 20 *l* bucket. In consolidated gravel, digging tools were needed to remove all material to a depth of 10-15 cm. Collection of a single sample required 5-15 min. The bucket was pulled or winched to the surface and transported to shore, where collected material was washed through a graduated series of sieves. The finest sieve had a mesh aperture of 4 mm. Material retained on each screen was examined for live mussels; 5-15 min were required to wash and pick each sample. Collected mussels were taken to a mobile laboratory, identified by species, and their shell lengths measured to the nearest 0.1 mm. Individuals not needed for voucher specimens were returned to the river.

Although the dive crew consisted of 3 - 4 individuals, only a single diver worked a site at a time. Support personnel consisted of 4 - 6 individuals that helped position boats and transport and process samples. Depending upon logistics and experience of personnel, 10 - 30 samples were collected and processed to completion each day.

RESULTS

SPECIES RICHNESS AND RELATIVE ABUNDANCE.

The cumulative number of species obtained at any site was a linear function of the logarithm of the number of quadrats sampled. This relationship is portrayed for representative high and low density sites located in beds in the Ohio and Mississippi rivers (Fig. 1). The dashed lines in figure 1

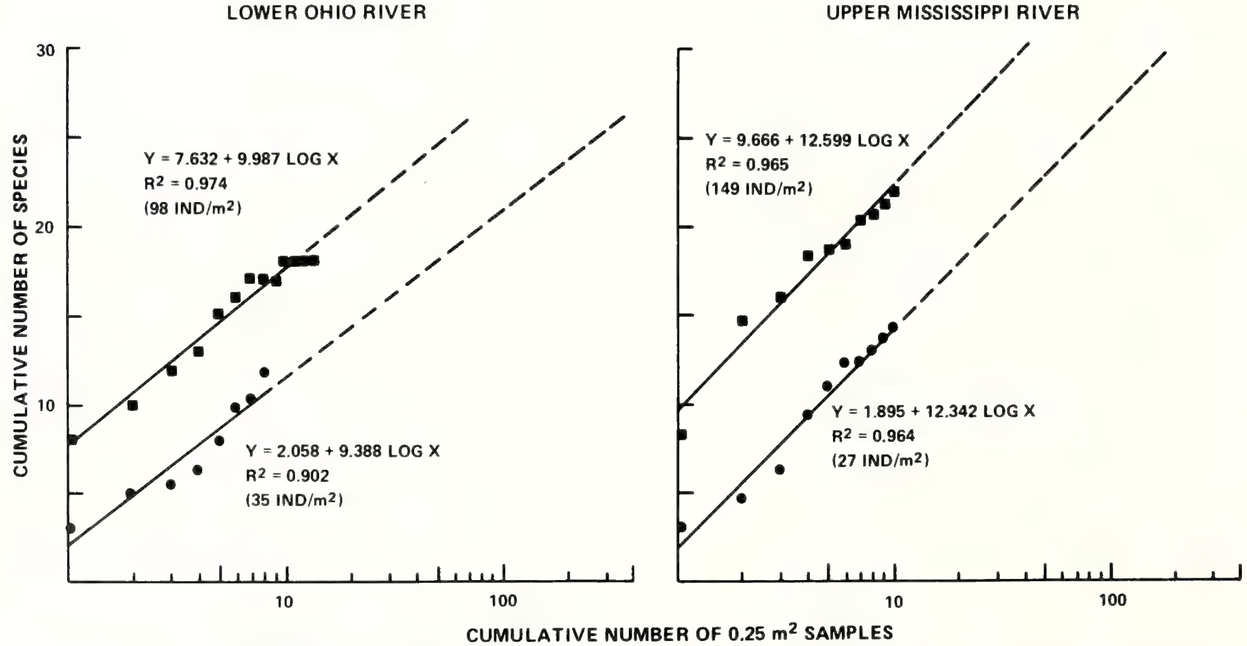

Fig. 1. Cumulative number of species in relation to number of quadrat samples collected in the Ohio and upper Mississippi rivers.

extend the number of samples beyond that which was collected in these surveys to a value necessary to obtain all species reported to exist in the beds in the Ohio (Miller *et al.*, 1986) and Mississippi rivers (Havlik and Stansbery, 1978). Extensions of these lines are not statistically valid in a strict sense. However, such extensions are instructive and supported by the ubiquity of relationships between estimates of species richness and the number of samples collected (McNaughton and Wolf, 1973). These relationships depict the diminishing rate of addition of new species as more samples are taken. For example, at a high density site in the Ohio River, 15, 21, 24, and 25 species were yielded by 10, 20, 40, and 60 samples, respectively. At a dense site in the Mississippi River, all species known from this reach of the river were collected with 40 samples; however, approximately 200 samples would be needed at the low density site to obtain all species present (Fig. 1).

A large number of quadrats must be sampled to obtain all species in both beds because most mussels are locally uncommon. Both beds were heavily dominated by a single unionid species. For example, *Amblema plicata* (Say) comprised 54.3% of the east channel community in the upper Mississippi River in 1985 and *Fusconaia ebena* (Lea) represented 66.7% of all native unionids in the Ohio River in 1985. Of the 29 species collected in the upper Mississippi River in 1985, 16 accounted for less than 1% of the community. *Lampsilis higginsi* (Lea), a species on the Federal list of endangered species, ranked 17th on the list and comprised 0.61 and 0.58% of the community in 1984 and 1985, respectively. Of the 23 species collected in the Ohio River during the 1985 survey, 11 accounted for less than 1% of all native unionids. *Plethobasus cooperianus* (Lea), a federally-listed endangered species was collected in this bed using qualitative techniques (Miller *et al.*, 1986), but was not obtained in quadrat samples during any year.

DENSITY

In the upper Mississippi River, the average density of all unionid species at the five sites sampled in 1984 and the two sites (consisting of three subsites) sampled in 1985 ranged from 22 ± 20 to 202 ± 36 individuals per m^2 (± standard deviation, N = 10 at each site or subsite). In the lower Ohio River, densities ranged from 47 ± 24 to 80 ± 20 (N = 6) in 1983, and 102 ± 30 (N = 13) in 1985, and 9 ± 3 to 31 ± 6 individuals per m^2 (N = 8 for eight sites and N = 4 for one site) in 1986.

A further illustration of the contagious nature of these molluscan communities is shown by the results of sampling along a transect within the bed in the Mississippi River (Fig. 2). The spatial heterogeneity of the bed directly affects the number of samples required to accurately estimate mussel density with a defined level of accuracy and precision. The number of samples required to estimate mussel density was determined by treating a set of replicate samples within a site as a pilot survey. To determine the number of quadrats necessary to achieve a desired precision of total mussel density a procedure from Green (1979:41) was used. This requires making an estimate of the mean and standard deviation of the population from preliminary sampling. The number of samples necessary to achieve a desired estimate of precision is a function of the variance of the pilot sample. For each of the 11 site-specific surveys in the upper Mississippi River we computed the number of samples necessary to estimate the average density of all mussels within either 10 or 30% of the actual average density with a 5% probability of being incorrect. We found that from 1.4 to 37.5 (mean = 12.2) samples were required to be within 30% and from 12.9 to 246.5 (mean = 109.8) samples were required to estimate to within 10% of the actual average density of all unionids at the 11 sites. The coefficient of variation of density estimates was lower at sites in the Ohio River than those in the upper Mississippi River. From 1.7 to 15.9 (mean = 6.2) samples were required to be within 30%, and from 19.2 to 143.0 (mean = 55.9) samples were needed to estimate to within 10% of the average density for the 14 sites in the lower Ohio River.

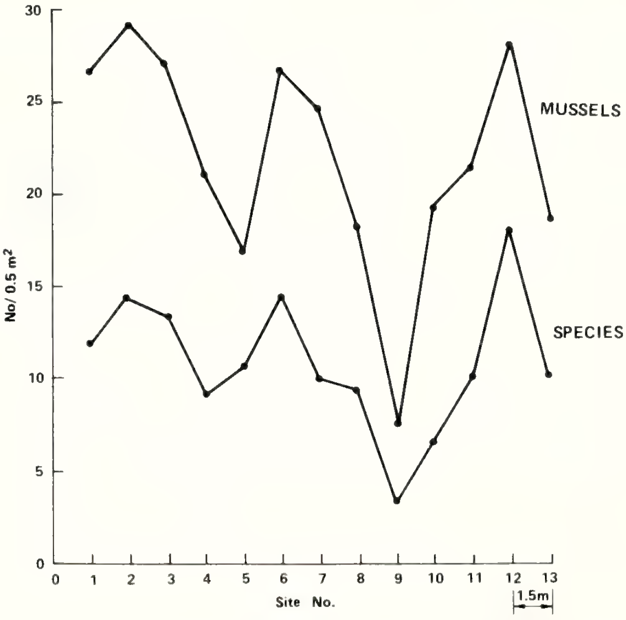

Fig. 2. Total individuals and species richness (pool for two 0.25 m^2 quadrats) from a transect in the upper Mississippi River.

SIZE DEMOGRAPHY

The most useful aspect of quantitative sampling was the detection of patterns in population recruitment for *Amblema plicata* in the Mississippi River and *Fusconaia ebena* in the Ohio River. The dominant species in both beds showed evidence of tremendous annual variation in recruitment strength. Mature females of both species produce glochidia each year for many years during their reproductive life span, and survival of glochidia through metamorphosis and settlement is contingent upon a number of abiotic and biotic variables. Thus, large annual variations in recruitment should be expected in such populations.

Shell length frequency histograms for *Amblema plicata* in the Mississippi River indicate that recruitment success was

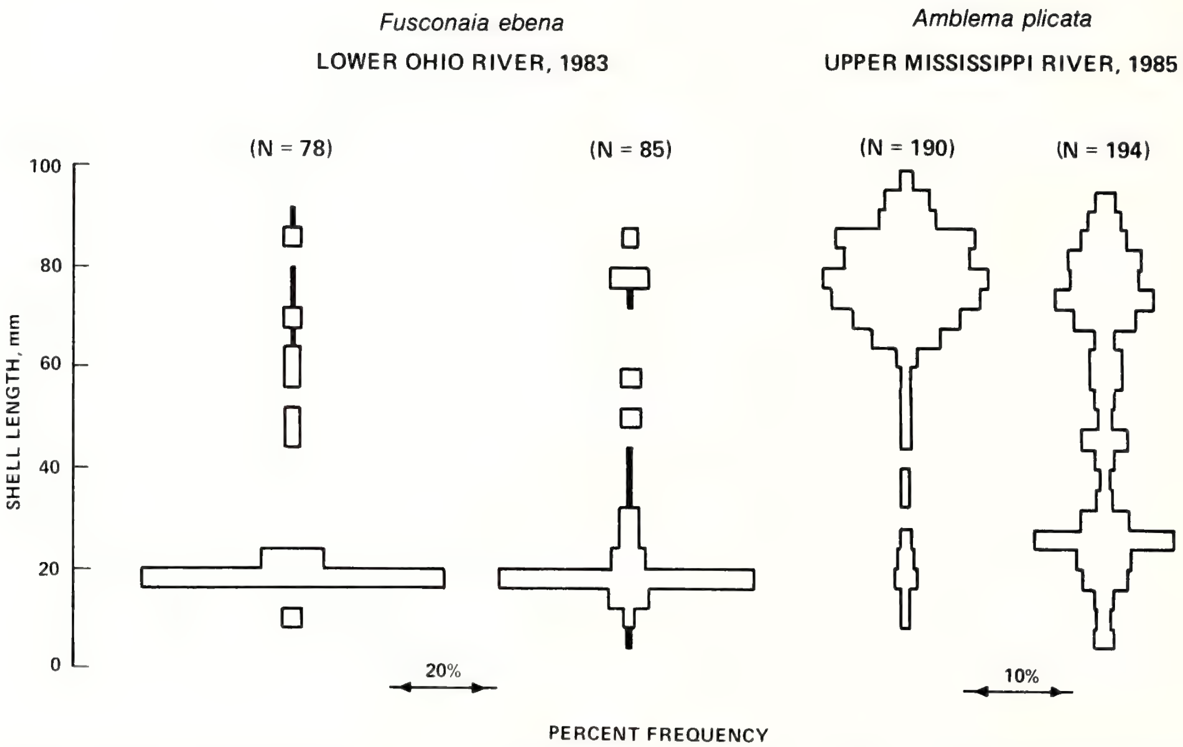

Fig. 3. Representative length-frequency histograms for *Fusconaia ebena* at two sites in the Ohio River in 1983 and *Amblema plicata* at two sites in the Mississippi River in 1984.

low for year classes represented by mussels between 40 and 60 mm in 1984 (Fig. 3). It is unlikely that selective mortality of these size classes occurred in the post-settlement stage of the life cycle. Also, recruitment exhibited spatial variability within the mussel bed. Although the sites in the Mississippi River depicted in figure 3 were less than 1 km apart, recruitment rates were not uniform throughout the mussel bed.

Intersite differences in patterns of size demography were not detected for *Fusconaia ebena* in the Ohio River (Fig. 3). However, evidence of annual variation in recruitment was more striking for *F. ebena* in the Ohio River (Fig. 3). In this population a single year class (probably 1982), represented by mussels 16-20 mm long, accounted for 70% of all individuals of this species collected in 1983. This same year class remained a dominant feature of the size demography of this population when assessed again in 1985 and 1986 (Fig. 4, cohort centered at 29 mm in 1985 and at 36 mm in 1986). Strong recruitment was not observed for any year class since 1982.

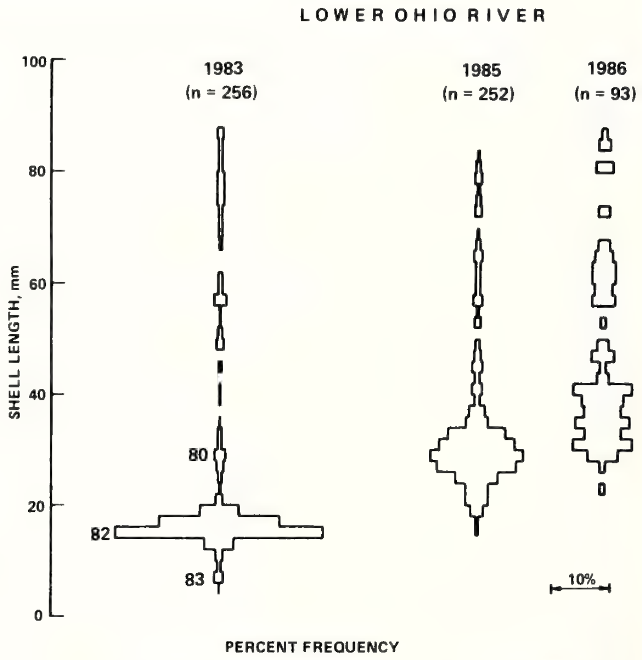

Fig. 4. Annual variation in recruitment for *Fusconaia ebena* in the lower Ohio River in 1983, 1985, and 1986.

DISCUSSION

The areas studied in the upper Mississippi River near Prairie du Chien, Wisconsin and the lower Ohio River near Olmsted, Illinois are among the most dense and rich mussel beds in these two rivers (Havlik and Stansbery, 1978; Miller *et al.*, 1986). Rigorous quantitative sampling at both beds revealed common features of community and population structure. Both communities are marked by heavy dominance by a single species and a large number of uncommon species. This same pattern is observed in most natural communities (e.g. Hughes, 1986). Based upon results of these studies, mussels in large rivers are no exception to this general rule.

Quantitative samples are required for unbiased estimates of the relative abundance of species. A consequence of the local rarity of many unionids is that a large number of quantitative samples are required to obtain all species at a site (see also Kovalak *et al.*, 1986). A combination of qualitative and quantitative sampling methods is the most efficient way to completely assess community composition. Qualitative surveys facilitate estimation of species richness, and quantitative surveys are required for estimation of relative species abundance.

Density of mussels is estimated with fewer samples than species richness and relative abundance. Based on our results, seven to twelve quadrat samples were sufficient to estimate the average density within 30% of the actual average density at a site with a 5% probability of being incorrect. As these statistics demonstrate, intersite variation in average density and the coefficient of variation of density estimates can be substantial. This is a direct consequence of the contagious nature of these communities and illustrates the need for a study design which includes adequate number of sites and replicates. Intrasite variation could be reduced by collecting individual samples within cells of a large (4m x 4m) 16-celled PVC grid secured to the bottom with pins. This procedure could help to eliminate diver bias and could reduce the coefficient of variation of estimates made of particularly contagious distributions.

Annual and intersite variation in recruitment was evident in both mussel beds. Intersite variation in patterns of size demography, like intersite variation in density, argues for sampling replicate sites. Annual variation in recruitment of dominant mussels, while evident in both beds, was particularly striking for *Fusconaia ebena* in the lower Ohio River. The size demography of this species was such that a single year class will remain a dominant feature of the size structure of this population for years hence.

Most riverine unionids have a long life span, take several years to mature, and appear to have great annual variation in recruitment success. These organisms are especially sensitive to commercial fishing and development of water resource projects. Regulation of commercial harvests and protection of habitat must be based on knowledge of population and community demographics. Currently we are conducting annual surveys at important mussel beds to monitor long-term trends in these parameters. However, most mussel studies in large rivers have not been sufficiently quantitative to elucidate important aspects of the biology of these invertebrates. Judgments on the condition of freshwater bivalves in large rivers should be based on quantitative substratum sampling that enables accurate determination of relative abundance, density, recruitment, growth, and mortality.

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SYMPOSIUM ON THE BIOLOGY OF THE POLYPLACOPHORA

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ROBERT C. BULLOCK
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ANCESTORS AND DESCENDENTS: RELATIONSHIPS OF THE APLACOPHORA AND POLYPLACOPHORA

AMELIE H. SCHELTEMA
BIOLOGY DEPARTMENT
WOODS HOLE OCEANOGRAPHIC INSTITUTION
WOODS HOLE, MASSACHUSETTS 02543, U. S. A.

ABSTRACT

Four organ systems, pericardium of primitive mollusks, shell ontogeny and spicule formation in chitons and aplacophorans, chaetoderm oral shield, and aplacophoran radula, are described and their relationships discussed. The discussion suggests: (1) a coelomate ancestor of the mollusks; (2) a polyphyletic origin of shell, one for Conchifera and another for chitons; (3) a single class Aplacophora containing two taxa, the Chaetodermomorpha and Neomeniomorpha; (4) an archimolluscan radula with a pair of separate radular membranes bearing rows of single teeth. Evidence is presented that contradicts the following hypotheses: (1) an acoelomate origin of mollusks; (2) the division of aplacophorans into two classes; (3) the derivation of the univalved molluscan shell from a common stem with the eight-shelled chitons. The concept of a subphylum Aculifera is rejected as unnecessary since it holds no essential information.

Hypotheses of early molluscan evolution in the last fifteen years have proposed an acoelomate, turbellariomorph pre-molluscan ancestor with a mucoid dorsal cover and a broad, ciliated locomotory sole through which opened a mouth (Fig. 1) (Salvini-Plawen, 1972, 1980, 1985; Haas, 1981; Boss, 1982; Poulicek and Kreusch, 1983; see also Fretter and Graham, 1962; Stasek, 1972). According to such theories, this pre-mollusk gave rise to an archimollusk with a spiculose integument, an unpaired radular membrane, and a mouth that opened through the ventral locomotory surface. The archimollusk then gave rise to two major taxa, the burrowing aplacophorans (Chaetodermomorpha = Caudofoveata) and an "adenopod", with seven transverse rows of scales and a head separated from the sole. The second group of aplacophorans, the footed Neomeniomorpha (= Solenogastres *sensu* Salvini-Plawen), have split off from the hypothetical "adenopod", the latter giving rise to an "archiplacophoran" with plates formed from coalesced scales. The "archiplacophoran" in turn was the precursor of the Polyplacophora on one hand and the rest of the shelled mollusks, the Conchifera, on the other (for recent accounts and bibliographic references, see Runnegar and Pojeta, 1985; Wingstrand, 1985; Salvini-Plawen, 1985). The subphylum Aculifera, recognized by Haas (1981) and formerly, but no longer, by Salvini-Plawen (cf. 1972, 1980), includes the extant Aplacophora and Polyplacophora as well as the hypothetical archimollusk, adenopod and archiplacophora; all other mollusks form the subphylum Conchifera. Salvini-Plawen (1980) considers the Chaetoder-

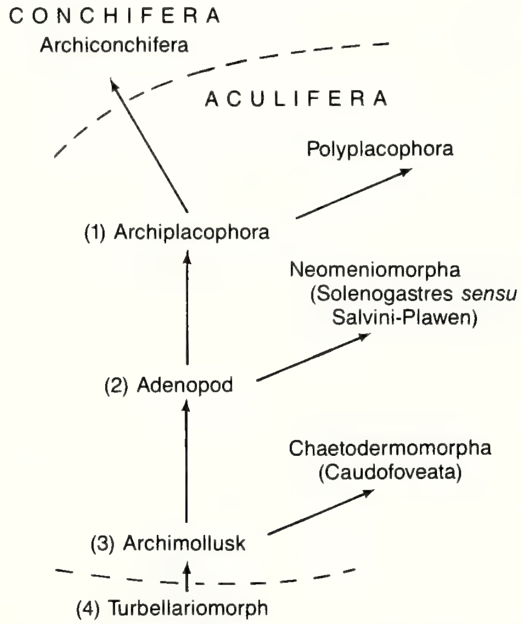

Fig. 1. Phylogeny of the Mollusca (adapted in part from Salvini-Plawen, 1980; Haas, 1981; Poulicek and Kreusch, 1983). Questioned in the text is the validity of: (1) an archiplacophoran origin of the Conchifera; (2) separation of the aplacophoran taxa Chaetodermomorpha and Neomeniomorpha by the existence of an Adenopod; (3) an archimolluscan radula with an undivided radular membrane; (4) an acoelomate ancestor. Compare with figure 14.

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momorpha to belong to the subphylum Scutopoda; all remaining mollusks, including the Neomeniomorpha, constitute the subphylum Adenopoda.

Evidence presented here draws on recent observations or experiments on shell and radula formation, the structure of the oral shield of the burrowing aplacophorans, and the size of pericardial spaces in three primitive molluscan classes. The evidence raises questions about the validity of four hypotheses: (1) there is a monophyletic (archiplacophoran) origin of chitons and conchiferan mollusks; (2) the two aplacophoran taxa belong to two separate classes; (3) the most primitive molluscan radula had an undivided radular membrane; (4) the ancestor of mollusks was acoelomate (Fig. 1).

SHELL AND SPICULES

APLACOPHORA AND POLYPLACOPHORA

The Aplacophora and Polyplacophora have been classified together either as the Amphineura because of their similar ladder-like nervous systems (not examined here), or as the Aculifera because of their similar integumental structures: papillae, spines, and cuticle. Indeed, these anatomical relationships between the two groups have been used to justify the inclusion of Aplacophora within the Mollusca (for historical reviews, see Hyman, 1967; Scheltema, 1978), although they are better regarded as symplesiomorphic traits, shared primitive states that do not necessarily show close evolutionary relationships.

Beedham and Trueman (1968) found similarities in the histochemistry of aplacophoran and chiton integumental cuticle and concluded that "the cuticle of the Aplacophora is tentatively equated with an early mucoid stage in the evolution of the molluscan shell... [The cuticle of *Acanthochiton*] has in addition a discrete inner cuticular layer which may act as a semi-conducting membrane in the deposition of calcareous plates" (p. 443). The papillae of Aplacophora and Polyplacophora are probably homologous (F. P. Fischer, pers. comm.); the papillae and aesthetes of Polyplacophora are likewise homologous (Fischer *et al.*, 1980; Fischer, 1988).

The process of calcareous spicule formation, most recently investigated by Haas (1981), is alike in aplacophorans and chitons (Fig. 2). In both taxa, a spine is secreted extracellularly within an invagination of a single cell. A basal cell secretes calcium carbonate, and as the spicule grows beyond this cell, a crystallization chamber is sealed off by a collar of neighboring cells. The megaspines in chitons, which do not occur in Aplacophora, are formed by a proliferation of the original single basal cell.

The attempt to find further similarities in calcium carbonate deposition that would link the Aplacophora and Polyplacophora by examining embryogenesis has led to less conclusive comparisons. Larval development in the two

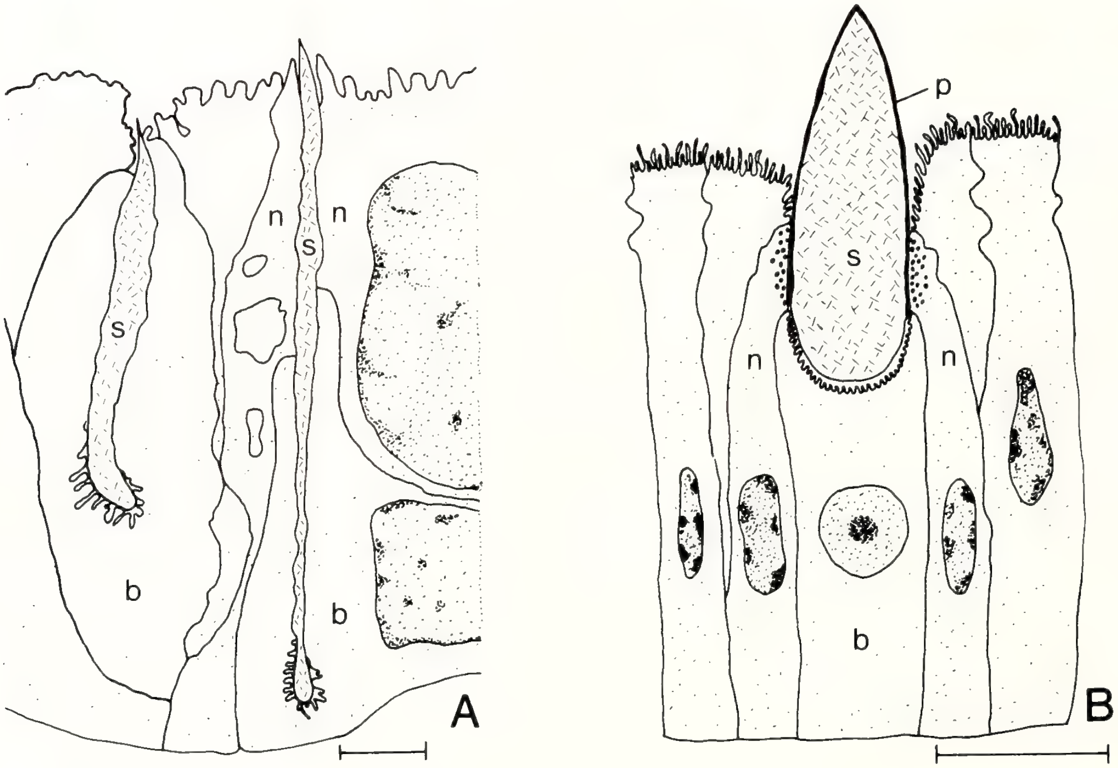

Fig. 2. Spicule formation in Aplacophora and Polyplacophora. **A.** Primitive Neomeniomorpha. **B.** *Lepidochitona cinerea* (Linnaeus). An organic pellicle has not been demonstrated around spicules of the Aplacophora. (After Haas, 1981.) (b, basal cell; n, neighboring cell; p, organic pellicle; s, spicule). Scale bars = 1 μm.

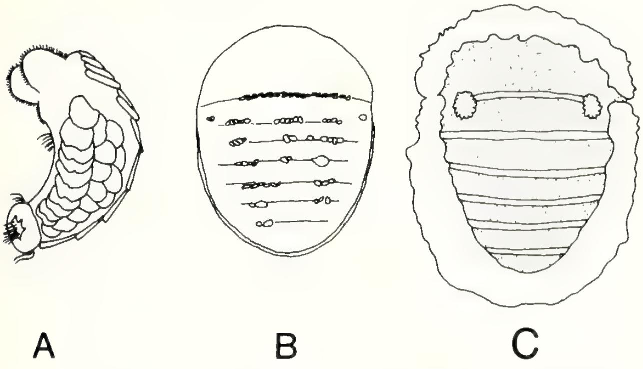

Fig. 3. Reported ontogeny in an aplacophoran, *Nematomenia banyulensis* Pruvot, and a chiton, *Lepidochitona corrugata* Reeve [= *Middendorffia caprearum* (Scacchi)]. **A.** Pruvot's larva, a single observation, lateral view, of a metamorphosing larva of *Nematomenia* with seven dorsal calcareous "'plaques', slightly imbricated and formed of rectangular, plainly juxtaposed spicules" (translated from Pruvot, 1890). The larva did not survive to a juvenile stage. **B.** Defective shell formation in *Lepidochitona corrugata* (= *Chiton polii* (Philippi) as illustrated by Kowalevsky (1883) with separate granules of calcium carbonate deposited along seven plate fields. Coalescence of these granules does not lead to normal growth of shell plates (see Kniprath, 1980). **C.** Birefringence under cross-polarized light in a normally developing *Lepidochitona corrugata* larva. Noncalcareous areas are stippled; the birefringent spicular girdle and six straight, uninterrupted anlagen of the shell plates are without stippling, as are the birefringent rosette-shaped larval eyes. (A and B after Salvini-Plawen, 1972: Fig. 29, after comparison with the original drawings of Pruvot, 1890, and Kowalevsky, 1883; C drawn after photograph by Kniprath, 1980: Fig. 1b.). Scales not known.

groups is dissimilar, but Salvini-Plawen [1972, 1980, 1985 (with qualifications)] argues for homology between seven rows of spicules seen once in a single aplacophoran larva [*Nematomenia banyulensis* Pruvot, Pruvot (1890)] and the development of shell in the larva of the chiton *Lepidochitona corrugata* (Reeve) (= *Chiton polii* Philippi) by a coalescence of granules (Fig. 3A, B) (Kowalevsky, 1883). The rows of spicules observed by Pruvot have not subsequently been seen in any other aplacophoran larvae [*Epimenia verrucosa* (Nierstrasz), *Halomenia gravida* Heath, *Neomenia carinata* Tullberg; see Hadfield (1979) for a summary]. Pruvot's drawing is a lateral view, and the often-copied dorsal view showing seven rows of spicules is a hypothetical reconstruction (Salvini-Plawen, 1972; Wingstrand, 1985).

Recently, Kniprath (1980) reported from rearing experiments that in the larvae of both *Lepidochitona corrugata* [=*Middendorffia caprearum* (Scacchi] and *Ischnochiton rissoi* (Payraudeau) the anlagen of the plates are secreted as uninterrupted rods along narrow transverse depressions, the shell or plate fields, after the development of girdle spicules (Fig. 3C). When *Lepidochitona* larvae were reared at temperatures of 14°-16°C, shell development was normal, but all larvae raised at higher temperatures of 18°-21°C were abnormal and developed granules similar to those reported by Kowalevsky (1883). These granules, even when they coalesced, produced defective shell plates.

The seven "plaques" of Pruvot's larval aplacophoran specimen are said to reflect the number of plates in the early fossil chiton *Septemchiton* (Hyman, 1967; Salvini-Plawen, 1980) and the seven "larval" plaques of chitons (Salvini-Plawen, 1985). However, Rolfe (1981) has shown that the most anterior plate of *Septemchiton*, a burrowing form, although greatly reduced is indeed present and that *Septemchiton* therefore has a full complement of eight plates. Although the caudal plate in chitons is usually added last during development, sometimes only after an extended period of five weeks (Pearse, 1979), it is not clear whether this time lapse reflects an ancestral chiton with only seven plates or is simply a result of development as a chiton elongates. In many adult aplacophorans with single overlapping layers of flat, leaf-like spicules, the bases of the spicules are aligned in rows that are transverse to the long axis of the animal (unpub. data); it would therefore not be surprising to find spicules lined-up in metamorphosing larvae that could be mistaken for "plaques".

Evidence for the coalescence of spines is said to be shown by three sets of broad spicules, or shields, on the head of the juvenile aplacophoran *Nematomenia protecta* (Thiele, 1913). This conclusion is based on spicule shape only, without reference to the underlying epithelium; the number of cells involved in secreting a "shield", a single cell or more than one cell, is not known, despite the inferred epithelial connection constructed by Salvini-Plawen (1985: Fig. 36D). The evidence for coalescence therefore remains unsubstantiated.

Both aplacophorans and chitons retain in common a phylogenetically early mode of calcium carbonate deposition in the form of spicules, but until further observations on aplacophoran embryogenesis prove to the contrary, close evolutionary relationship between the formation of aplacophoran spicules and chiton shells is considered undemonstrated. There is no evidence within chitons themselves that spicules have coalesced to form shell plates.

POLYPLACOPHORA AND THE OTHER SHELLED MOLLUSKS (CONCHIFERA)

The process of shell formation in chitons is argued here to be unique among mollusks. In those gastropods, bivalves, and cephalopods for which the entire shell ontogeny has been studied, earliest calcium carbonate deposition is preceded, first, by formation of a shell-field and shell-field invagination from part of the dorsal ectoderm and, second, by the secretion of an organic pellicle, usually equated with periostracum, over the invagination (Fig. 4A) (Kniprath, 1981; Eyster and Morse, 1984). [In the Cephalopoda, yolk interferes with invagination and, instead, ectoderm builds up in an elevated ring (Kniprath, 1981)]. Calcium carbonate is then secreted beneath the organic pellicle. In the nudibranch *Aeolidia papillosa* (Linnaeus), the early organic pellicle is overlain by long cytoplasmic processes that presumably seal off the crystallization chamber under the pellicle (Fig. 4B) (Eyster and Morse, 1984).

In chitons, no shell field invagination forms (Fig. 4C).

Deposition of a shell plate anlage takes place within a transverse depression bounded and sealed off by long, overlapping microvilli that lie beneath a gelatinous mucoid substance, certainly not periostracum, and questionably equated with a cuticle (Fig. 4C, D) (Kniprath, 1980; Haas *et al.*, 1980; Haas, 1981).

Not only are the ontogenetic processes of shell formation different in chitons and the Conchifera, but structures of the fully formed shells are also unlike and homologies are difficult to discover. Periostracum in the Conchifera, a structure conservative in manner of its secretion and in composition (Grégoire, 1972), does not exist in chitons, although Haas (1981) has demonstrated the presence of a thin cuticle, or properiostracum, overlying the tegmentum and a properiostracal groove surrounding each shell plate. There is no nacreous layer in chiton shells as found in other mollusks, and the cross-lamellar structure of the shell plates is crystallographically unique, with bundles of crystal fibers in the lamellae ordered so that their c-axis "coincides with the bisectrix of these crossing fibers" (Haas, 1981: 403) and the "whole complex acts crystallographically as a single crystal" (Haas, 1977: 392). In other molluscan cross-lamellar structures, the angle between crystal fibers is about 110°; in gastropods they lie between 90°-130° (Wilbur and Saleuddin, 1983). Haas (1981) considered the cross-lamellar structure of chitons to be homologous with the nacreous layer of other shelled mollusks and imagined that both arose from an undifferentiated inner layer of the "archiplacophoran" plates. The shell of the Conchifera became univalved he believed by fusion of the shell and shell fields. There is no evidence, however, that the dynamics involved in the process of earliest shell deposition through the interplay of shell-field invagination and pellicle in Conchifera could have evolved from the very different process of shell-plate production found in chitons.

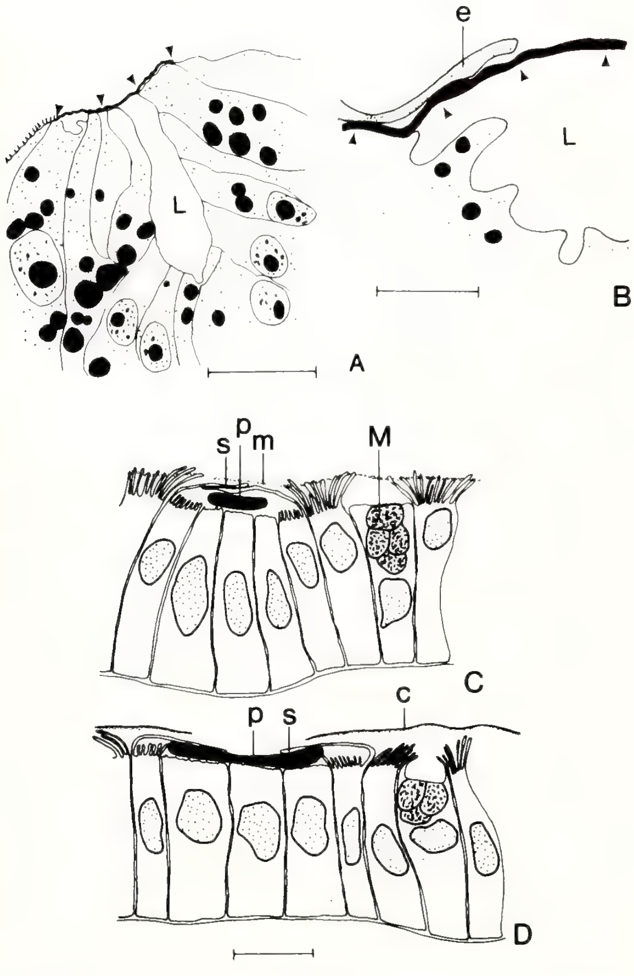

Fig. 4. Larvel shell deposition in (A, B) the gastropod *Aolidia papillosa* (Linnaeus) and (C, D) the chiton *Ischnochiton rissoi* (Payaudreau). In A, an organic pellicle (arrows) covers the lumen of the shell field invagination (L); in B, the edge of the pellicle can be seen to be overlain by a cytoplasmic extension (e). Calcium carbonate has not yet been deposited. (Drawn after photographs in Eyster and Morse, 1984: Figs. 1, 2). In C, calcium carbonate of the shell plate (p) has been deposited under the overlapped microvilli (s, "stragulum"); a mucus layer (m) covers the stragulum. In D, microvillar processes (s) have pulled apart and a cuticle (c) with a contrasted outer layer is beginning to form; M is perhaps a mucus cell (C and D after Kniprath, 1980.) Scale bars: A = 10 μm; B = 0.5 μm; C; D approximately 6 μm.

Thus, recent work on the ontogeny and structure of shell in chitons and Conchifera shows such major differences between them that it can be questioned whether there was a monophyletic origin of molluscan shell, or rather one origin for chitons and a second for the remaining extant and extinct Conchifera. Tubules in the shells of the monoplacophoran *Neopilina* (Schmidt, 1959), bivalves (e.g. Waller, 1980), and gastropods have sometimes been considered homologous with the aesthete canals of chitons and argued as a support for a monophyletic origin of molluscan shell (e.g. Salvini-Plawen, 1985), but the homology is so far uncertain. When the ontogenetic development of *Neopilina* becomes known, perhaps a basis will be found for deciding whether molluscan shell has a monophyletic or polyphyletic origin.

CHAETODERM ORAL SHIELD AND THE ARCHIMOLLUSK

One of the original arguments for dividing the Aplacophora into two classes and, ultimately, into two subphyla depends on the hypothesis that mollusks have a turbellariomorph, or flatworm, ancestry. This phylogeny is based on a supposed homology and similarity in mode of locomotion between mollusks and flatworms by means of a "ventral mucociliary gliding surface" (Salvini-Plawen, 1972, 1980: Fig. 5, 1985; see also Trueman, 1976). The molluscan archetype, like the flatworms, is said not to possess a separation of the head from the foot, and the mouth consequently opens through the sole; innervation of the sole is said to be from both the cerebral ganglia and ventral nerve cord. [Stasek (1972) has illustrated but not discussed a head separate from the locomotory sole in the turbellariomorph molluscan precursor.]

Support for the flatworm-like archimolluscan locomotory ventral surface is said to be shown by the cerebrally innervated oral shield of the burrowing Chaetodermomorpha (= Caudofoveata) (Fig. 6A); that is, the shield is regarded as a remnant of the original gliding surface (Salvini-Plawen, 1972, 1980, 1985). The homology with a creeping sole was originally based on histologic similarities in the morphology and arrangement of nerve and mucous cells that lie in the epidermis beneath the oral shield cuticle of chaetoderms and the spiculeless cuticle within the foot-furrow of the creeping neomeniomorphs [Hoffman, 1949; for a translation and explanation, see Scheltema (1983)]. The homology, however, is spurious since molluscan ectoderm, with or without cuticle, is richly supplied with both nerve and mucous cells. Furthermore, Salvini-Plawen (1985) has described (but not illustrated) the specialized ultrastructure of the oral shield, consisting of interdigitated microvilli with glycocalyxes and supporting fibers.

The oral-shield cuticle and epithelium in six genera (*Scutopus, Limifossor, Prochaetoderma, Metachaetoderma, Falcidens,* and *Chaetoderma*) representing all families of chaetoderms are continuous with pharyngeal (oral tube) cuticle and epithelium (Scheltema, 1981, 1983). Light microscopy does not reveal a border where the oral shield cuticle joins the pharyngeal cuticle (Figs. 5, 6B), but ultrastructural studies would define this area better. *Scutopus* is considered to be the most primitive chaetoderm because of its least differentiated midgut (Scheltema, 1981) and because of the evidence of ventral fusion of the cuticle (Salvini-Plawen, 1972). In this genus only scattered pyriform mucous cells open through the oral shield, further refuting Hoffman's homology, which likened the lobes of mucous cells opening at the lateral edges of the oral shield in advanced Chaetodermatidae with the pedal gland of Neomeniomorpha. This important aspect of Hoffman's homology linking lobed mucous cells of the oral shield and foot furrow was ignored by Salvini-Plawen (1980) while retaining the homology itself. Definitive evidence that the oral shield is a part of a vestigial ventral sole would require innervation from the ventral (= pedal) nerve cord rather than from the cerebral ganglia.

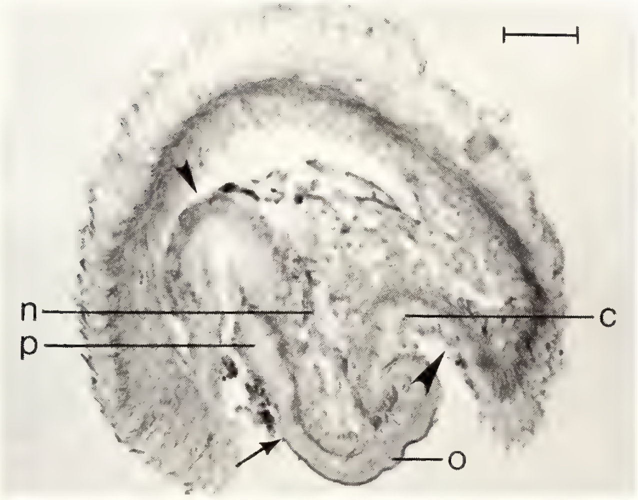

Fig. 5. Oral shield of a Chaetodermomorpha: section through the mouth, pharynx, and oral shield of *Scutopus megaradulatus* Salvini-Plawen showing continuous cuticle of pharynx and oral shield (from 650 m off Cape Hatteras, North Carolina, U. S. A., 34°14.8'N, 75°46.7'W; fixed in formalin, preserved in alcohol, stained with haemotoxylin/Gray's double contrast, sectioned at 0.7 µm.) (c, spiculose cuticle of integument; n, nerve fibers from precerebral ganglion; o, cuticle of oral shield; p, cuticle of pharynx). Small arrow indicates change from oral shield cuticle with a thickened outermost layer to homogeneous cuticle of pharynx. Scale bar = 0.05 mm.

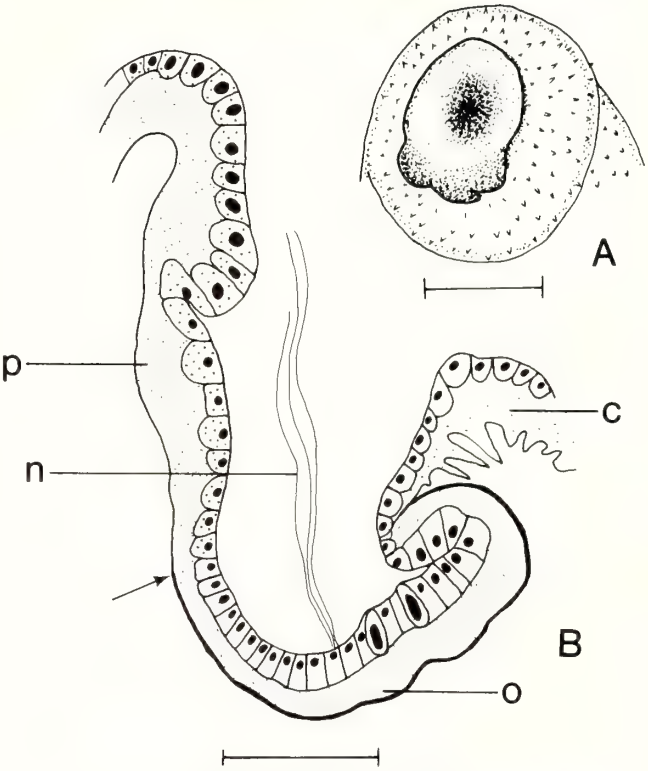

Fig. 6. Oral shield of *Scutopus megaradulatus*. **A.** Anterior view of oral shield *in situ* surrounding darkened mouth in center. **B.** Semischematic drawing of area between large arrowheads in figure 5 showing histology of pharyngeal and oral shield cuticle (lettering and small arrow as in Fig. 5). Scale bars: A = 0.3 mm; B = 0.05 mm.

Thus, the oral shield of the Chaetodermomorpha is considered here to be an autapomorphy, a cerebrally innervated external continuation of pharyngeal cuticle like a lip belonging to the head, not to a ventral sole. There is no convincing evidence that it is a remnant of an original creeping sole homologous to the ventral surface of a turbellarian flatworm. The separation of the Aplacophora into two classes based on the supposed (1) plesiomorphy of ventral innervation of the chaetoderm oral shield by the cerebral ganglia and (2) apomorphy of a head separate from the foot in the neomenioids and all other mollusks except chaetoderms is unsatisfactory. A head separate from the foot is considered here to be a plesiomorphy shared by mollusks generally but lost in the bivalves and, because of their burrowing habit, also in the chaetoderms.

RADULA

APLACOPHORAN RADULA

Evidence from the radula morphology of aplacophorans and from the ontogeny of gastropod and chiton radulae suggests that the molluscan radula orginated as a paired structure.

The radula in chitons, the monoplacophoran *Neopilina*, gastropods, and scaphopods is a chitinous structure formed of a single continuous ribbon, or radular membrane, which bears serial rows of teeth; both ribbon and teeth are continually secreted at the proximal end of a pharyngeal diverticulum, the radular sac (Fretter and Graham, 1962; Kerth, 1983; Scheltema, unpub. data). Each row of teeth has left and right sides and usually a central, or median, tooth. The radula is bilaterally symmetrical around the central tooth, that is, the teeth of each side are mirror images of one another. Along the length of the ribbon each tooth has the same shape as the tooth in front of and behind it, that is, the rows of teeth are serially repeated.

In the Aplacophora, the radula is formed in the usual manner and is likewise bilaterally symmetrical and serially repeated (Figs. 7A, 8A, C). The radula has been called monostichous or monoserial if there is only a single tooth in a row; with two mirror-image teeth in each row, distichous or biserial; and with more than two mirror-image teeth, polystichous or polyserial (Nierstrasz, 1905).

The usual type of radula in the Aplacophora is distichous; a central tooth is lacking in nearly all species. Unique among mollusks the radular membrane itself is divided down the middle so that the entire radula is a bipartite, bilaterally symmetrical, serial structure consisting of two strips

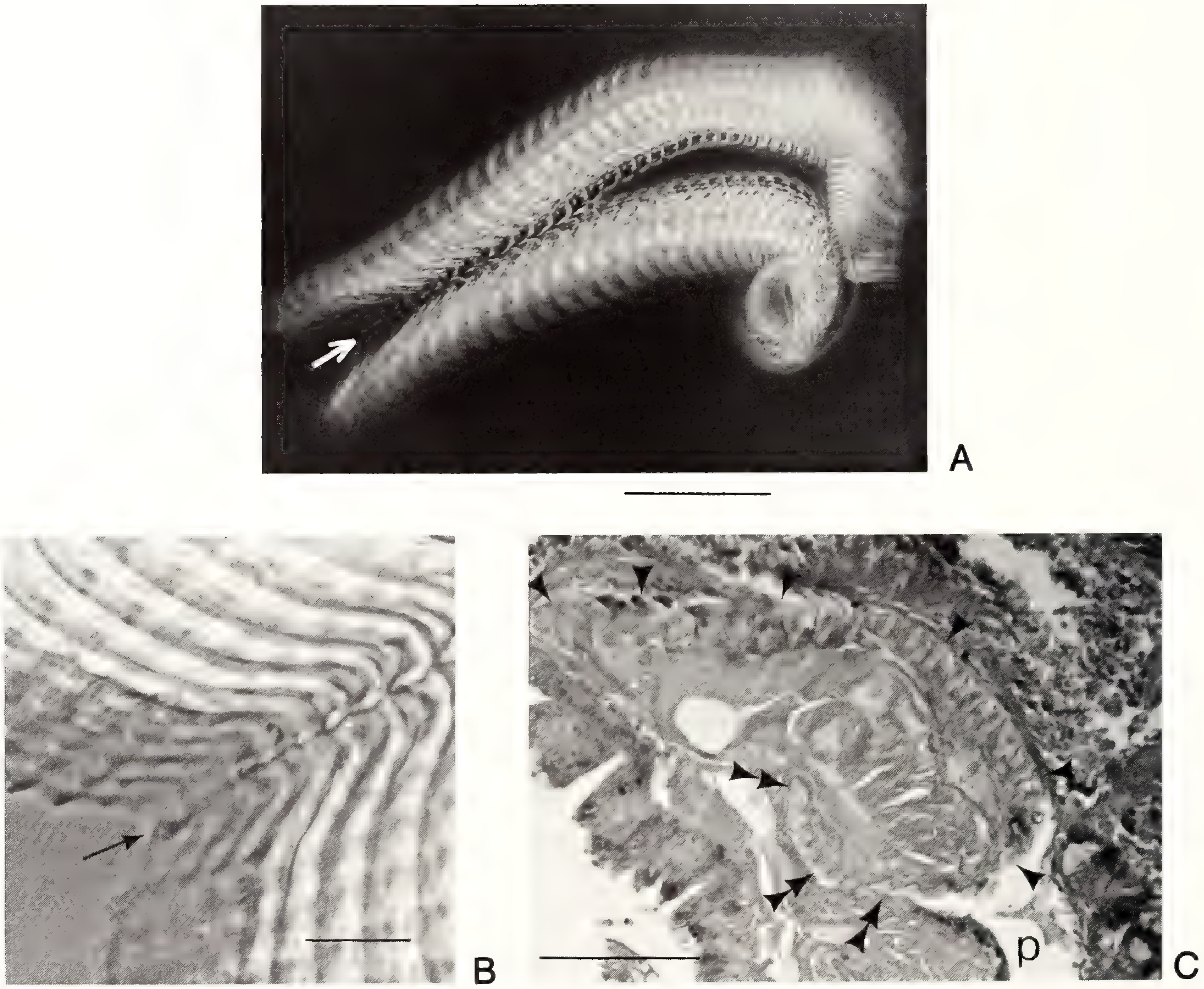

Fig. 7. Aplacophoran radula of *Simrothiella* species. **A.** *Simrothiella* sp. *b* (undescribed); at left are the newest, proximal teeth and fused radular membrane (arrow); distally (on the right) the membrane is bipartite and spirals ventrally down into two ventral pharyngeal pockets. **B.** Close-up of fused, proximal end of radula shown in A. (Whole amount in glycerine; see Scheltema, 1981, for dissecting technique). **C.** *Simrothiella* sp. *a* (undescribed), sagittal section through one side of radula, indicated by single arrowheads; double arrowheads show radula within the ventral pharyngeal pocket (Specimens from 2,633 m at 20º50'N, 109º 0.6'W; sections treated as in Fig. 5). Scale bars: A = 100 µm; B = 30 µm; C = 100 µm.

of continuous ribbon, each strip with rows of single denticulate teeth which are the mirror image of the opposed teeth (Figs. 7A, 8A, C). The two parts of the radular membrane are fused to a greater or lesser extent lengthwise along their medial (inner) edges forming a one-piece, unipartite radular ribbon along part of its length (Figs. 7B, 8A; Scheltema, 1981).

The structure of the radula is clear only when it is dissected and isolated from surrounding tissue (Scheltema, 1981). Reconstructions from histologic sections have resulted in misconceptions of actual structure and probable modifications during its evolution [e.g. Nierstrasz, 1905; Salvini-Plawen, 1972, 1978 (*Simrothiella*), 1985].

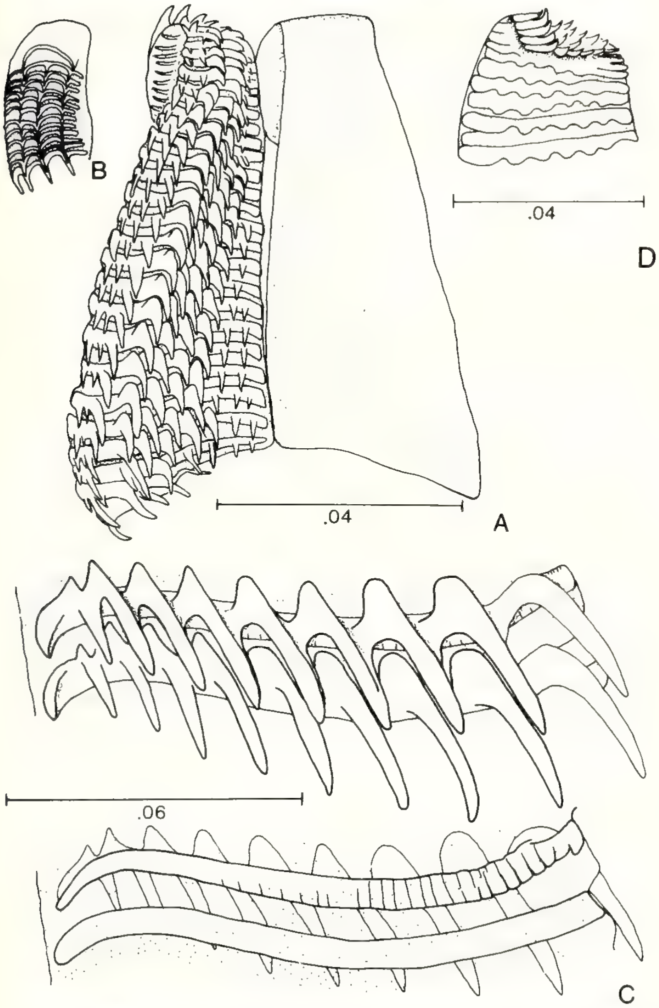

Fig. 8. Radula of *Simrothiella* sp. *b* (undescribed), radular membrane indicated by stippling. **A.** Entire radula of a juvenile specimen, dorsal view, anterior (oldest teeth) at top. Teeth of only left half of radula shown; teeth on the right are the mirror-image of those on the left. Denticles are added to the teeth medially as the radula widens and lengthens. **B.** Distal, oldest part of left radular strip shown folded under in A from ventral pharyngeal pocket; original, first-formed tooth is retained. **C.** Two views of the same two adjacent teeth from an adult specimen: upper teeth drawn in dorsal view as if they were on the right side of the radula, medial denticles on left; lower teeth from left side of radula drawn from beneath radular membrane. **D.** Most anterior part of the same adult radula from which teeth in C were drawn; comparison with juvenile radula B indicates that there is dissolution at the distal end of the radula within the ventral pharyngeal pocket (Specimens from 2,633 m at 20°50'N, 109°06'W). Scale bars in mm.

In order to differentiate the two states that exist for the radular membrane among mollusks, the terms "bipartite" and "unipartite" are used here, and the terms using "—stichous" are reserved for descriptions of the radular teeth only. Thus, a distichous radula can be either uni- or bipartite, but a monostichous radula is necessarily unipartite. The terms with "—serial," which should mean "arranged in series," are not used here, thus obviating the confusion of such a description as "monoserial with paired teeth."

As in other radulate Mollusca, the radular membrane in Aplacophora appears to migrate forward as teeth are added by the odontoblasts; in most species the membranes turn anteroventrally into paired or unpaired ventral pharyngeal pockets, where dissolution of the radula apparently occurs (Figs. 7C, 8D). Unlike grazing gastropods and chitons, in all but one family of Aplacophora the teeth show no wear and thus do not rasp.

The entire radula of juvenile specimen of *Simrothiella* (0.9 mm in length) has been examined. Within each ventral pharyngeal pocket is preserved the earliest ontogenetic development; the first tooth is a nondenticulate bar on a wide expanse of radular membrane (Fig. 8B). As the radula grows in length and width, denticles are added to the teeth medially, i.e. at their inner edges (Fig. 8A). Histologic cross-sections through the proximal, blind end of the radular sac show odontoblasts in two discrete groups, each presumably bound by basement membrane (Figs. 9, 10). The two groups lie within a single sac, surrounded in the usual manner by muscle.

Within the Aplacophora, the radula has evolved at least twice from having a bipartite, distichous radula (Figs. 7, 8) to a radula with a unipartite radular membrane. In the Dondersiidae (Fig. 11), the radula is altogether absent or consists of

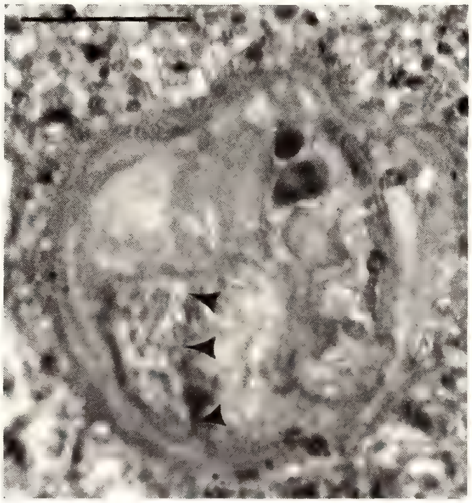

Fig. 9. Radular sac of *Simrothiella* sp. *a* (undescribed). Anterior view of somewhat oblique cross-section through proximal end showing membranes (arrowheads) bounding right and left groups of radula secretory cells (Specimen from 2,633 m at 20°50'N, 109°06'W). Scale bar = 35 μm.

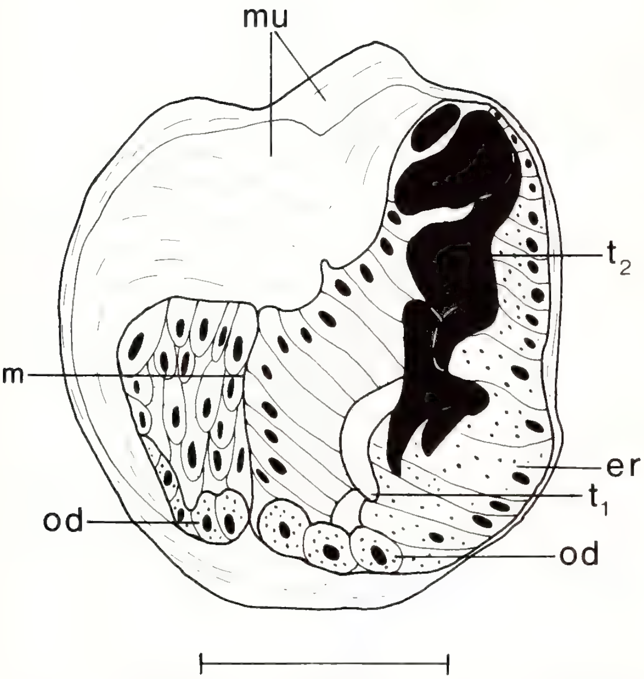

Fig. 10. Semischematic representation of radular sac cross-section shown in figure 9 (er, epithelium of radular membrane; m, membranes bounding left and right groups of radula secretory cells; mu, muscle; od, odontoblasts; t_1, early tooth, or perhaps denticle, not yet staining with haemotoxylin; t_2, older tooth stained by haemotoxylin). Scale bar = 35 μm.

only a few rows of single teeth, usually 6 or fewer. Its monostichous form appears to be the result of reduction and fusion of a distichous radula, with two of its paired denticles fused at tip and base. In the Prochaetodermatidae, the radula has evolved into a rasping structure with a unipartite radular membrane and a central tooth, or plate (Fig. 12) (Scheltema, 1981,1985).

There are no distinctive radula characteristics, synapomorphies, held in common or uniquely by the Aplacophora and Polyplacophora, the latter with rows of usually 17 teeth on a unipartite radular membrane.

ONTOGENY OF GASTROPOD AND CHITON RADULAE

Vestiges of an original distichous molluscan radula exist in the ontogenetic development of the chiton, pulmonate, opisthobranch, and prosobranch radula. The details of the developing chiton radula are treated by Eernisse and Kerth (1987) and Kerth (this symposium). The radula starts as rarely one to usually three pairs of lateral teeth on a unipartite radular membrane with a central tooth added later. In the ontogenetic development in five families and seven species of pulmonates, the radula begins as a distichous structure with two longitudinal rows of lateral teeth on a unipartite radular membrane; further laterals are then added, and finally a central tooth, which originally may be paired, is secreted thereby uniting the cross-rows (Kerth, 1979). Pruvot-Fol (1926) figured the earliest radular teeth of the opisthobranch *Polycera*,

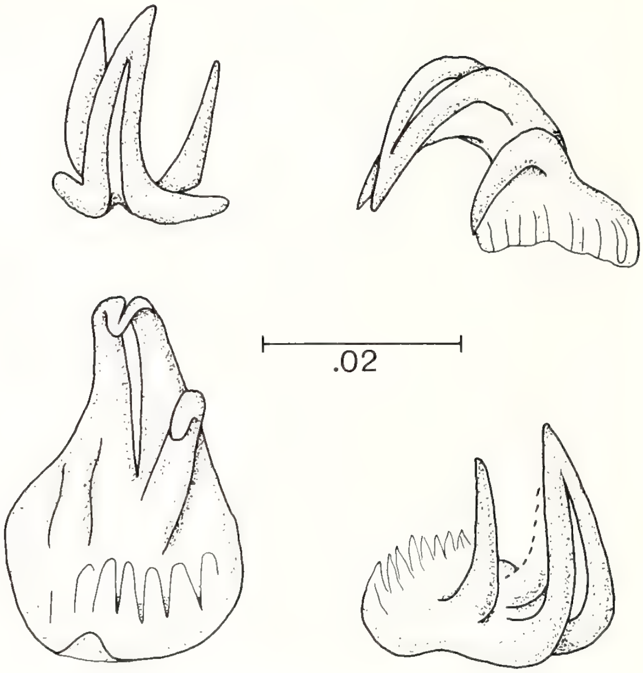

Fig. 11. Monostichous aplacophoran radula of an undescribed species of Atlantic Dondersiidae, four aspects; radular membrane not shown. One denticle is missing from the teeth in the lower two drawings (Specimen from 805 m, 39°51.3'N, 70°54.3'W). Scale in mm.

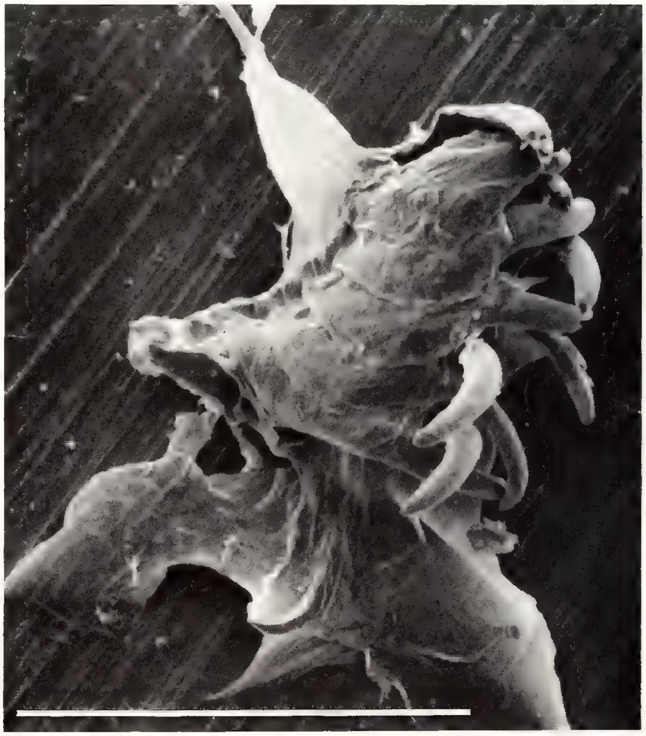

Fig. 12. Undivided, unipartite radular membrane of an undescribed species of Prochaetodermatidae; view of ventral surface (Specimen from 1,624 m 10°30.0'N, 17°51.5'W). Scale = 250 μm.

distichous with a "gouttiere" between them. The radular sac in the opisthobranch *Rhodope* (Riedl, 1960) and in the pulmonate *Physa* (Wierzejski, 1905) originates as a pair of invaginations. In *Rhodope*, lacking a radula, the paired invaginations are lost; in *Physa*, they unite to form a single sac. The developing radular sac in prosobranchs is often bifid (Fretter and Graham, 1962: 173).

To summarize, the most generalized aplacophoran radula is unique because it has a bipartite radular membrane with distichous teeth. Distichous teeth on a unipartite radular membrane exist ontogenetically in other molluscan groups.

PERICARDIUM

The pericardium is a space lined by mesoderm arising embryologically from cell 4d; therefore, it may be considered to be coelom. Raven (1966) questioned, however, whether coelomic cavities among mollusks arise from mesodermal bands (schizocoels) as they do among the annelids. [For an extensive overview of gonopericardial complexes within mollusks, see Wingstrand (1985)].

Salvini-Plawen (1968) hypothesized that the pericardial space evolved within the mesenchyme after the heart, surrounding it and thereby improving its function. Stasek (1972: Fig. 1A, B) illustrated such a situation in the molluscan precursors. Although the pericardium is relatively small in most gastropods and bivalves, in the three primitive classes Aplacophora, Monoplacophora, and Polyplacophora it is spacious relative to the size of the heart (Fig. 13). In *Neopilina* the pericardium is paired, and in the aplacophoran Chaetodermomorpha and most Neomeniomorpha it has either small or large, paired lateral extensions ("horns" in early literature), whose function is not known. Ontogenetically, in the single species of aplacophoran for which size during development is mentioned (Baba, 1938), the pericardium is already large before the heart develops.

How the pericardium functionally could have evolved in a pre-mollusk as a small space, then have become spacious and probably paired, and finally again become reduced in size, is difficult to imagine. Moreover, during organogenesis, the pericardium develops before the heart and the heart arises

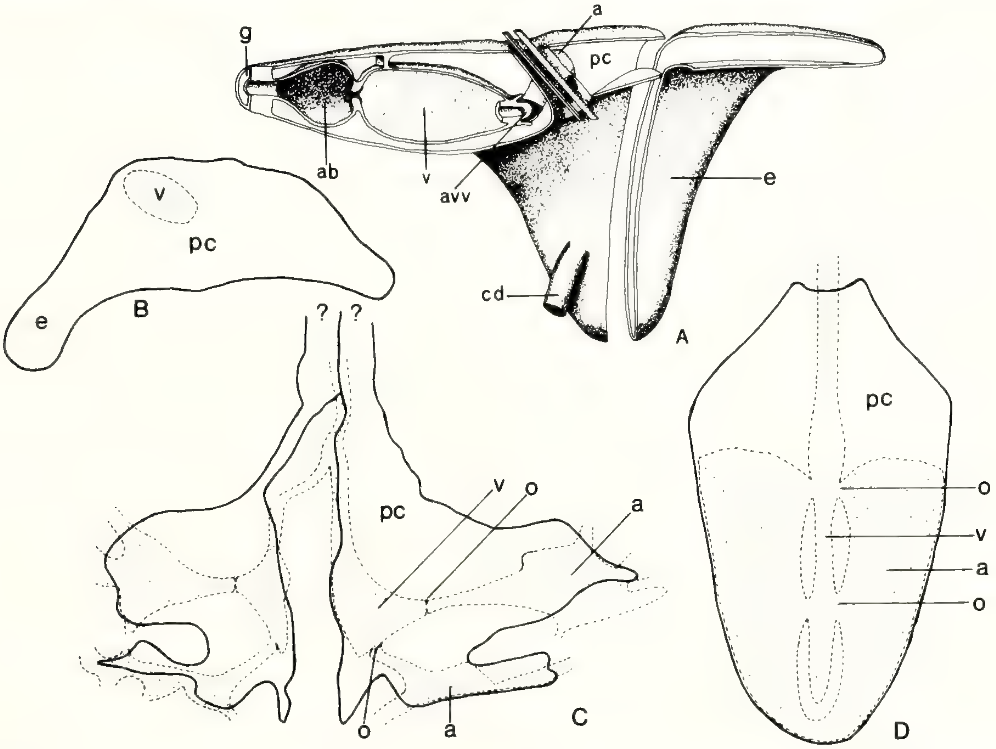

Fig. 13. Heart and pericardium in the primitive molluscan classes Aplacophora (A, B), Monoplacophora (C), and Polyplacophora (D) showing large pericardial spaces in relation to the size of the heart. In B, C, and D the heart is stippled and the pericardium is blank. **A.** *Chaetoderma nitidulum* Lovén, sagittal section through pericardium, heart, and gonopericardial duct (after Scheltema, 1972). Paired auricles (a) open into the ventricle on each side of an atrioventricular valve (avv). Gonads empty through paired ducts (g) into the pericardium (pc), and coelomoducts (cd) lead from the pericardium to the cloaca (not shown). The large paired lateral extensions of the pericardium (e) are known as "horns" in the older literature. **B.** *Simrothiella* sp. *a* (original drawing), same specimen as in figure 9. Somewhat oblique cross-section through the pericardium (pc), ventricle (v), and lateral extension of the pericardium (e). **C.** *Neopilina galatheae* Lemche, dorsal view (after Lemche and Wingstrand, 1959). The pericardium (pc) and ventricles (v) are paired; two pairs of auricles (a) open into each ventricle. It is not known whether there is a connection between the pericardia and gonads (see Wingstrand, 1985). **D.** *Acanthopleura echinata*, dorsal view (after Plate, 1898). Two pairs of ostia (o) open on each side into the ventricle (v); the number of ostia varies from one to four pairs, according to species (a, auricle; ab, aortal bulb; avv, atrioventricular valve; cd, coelomoduct; e, lateral extension of pericardium; g, gonopericardial duct; o, opening between auricle and ventricle; pc, pericardium; v, ventricle). Scales not indicated.

from the dorsal or inner epithelium of the pericardium (Baba, 1938; Raven, 1966), suggesting that evolution of the pericardium probably preceded that of the heart. The large pericardial spaces in the Aplacophora, Monoplacophora, and Polyplacophora point to a coelomate rather than to an acoelomate, turbellariomorph ancestor and lead one to re-examine the evidence for ancestral relationship between the annelids and mollusks (see Vagvolgyi, 1967; Wingstrand, 1985).

DISCUSSION

ACOELOMATE VERSUS COELOMATE MOLLUSCAN ORIGINS

The hypothesis that the ancestor of mollusks was acoelomate is rejected in favor of a coelomate origin because: (1) primitive molluscan taxa have large pericardial spaces; (2) evidence is lacking that the pericardial space began as a small opening in mesenchyme lined by mesoderm; (3) Wingstrand's evidence (1985) strongly suggests a molluscan "derivation from advanced oligomeric Spiralia ('proto-annelids' or 'proto-articulates')" (p. 8) (Fig. 14).

The existence of large pericardial spaces in the primitive extant mollusks has not been considered in hypotheses of an acoelomate molluscan origin. Rejection of the hypothesis of reduced metamery as the origin of molluscan coelom is probably correct (Salvini-Plawen, 1968); however, one need not suppose, therefore, a total absence of either coelom or metamery. Reiger (1985), after careful comparative studies of the fine structure of acoel connective tissue, argued that the acoelomate Bilateria themselves are derived through progenesis from a coelomate ancestor.

SHELL AND SPICULES

The Aplacophora probably evolved from a shell-less rather than from a shelled ancestor. Evidence for this assertion comes from properties of the cuticle (see SHELL AND SPICULES above) and from a comparison of numbers of dorsoventral muscles that run between the outer body wall and foot among various mollusks. In the Neomeniomorpha, two bilateral sets of oblique bands are repeated serially along the body; they are considered homologous to the dorsoventral pedal muscles in other mollusks (Salvini-Plawen, 1972). The evolution of dorsoventral musculature, which coevolved with the shell, has been toward reduction in number, from eight in Polyplacophora and tryblidian Monoplacophora to one in most Gastropoda. The serial arrangement of numerous bands in the Neomeniomorpha is considered therefore to be a plesiomorphy that preceded shell development and its consequent reduction of dorsoventral musculature.

No convincing published evidence links the process of extracellular spicule formation by a single cell (Haas, 1981) with the development of shell fields and shell deposition. The only common attribute of spicule and shell formation is that both are extracellular deposits of calcium carbonate.

Three types of calcium carbonate coverings are found in the Mollusca: spicules in Aplacophora and Polyplacophora; the shell plates of the Polyplacophora with a thin (nonperiostracal) organic cover, tegmentum, and hypostracum; and the conchiferan shell with periostracum, prismatic layer, and nacreous layer. The trend has been to treat these calcium carbonate structures as homologous, with a morphocline leading from spicules to plates by coalescence in chitons (e.g. Salvini-Plawen, 1972), and from the 8 shell fields in chitons to the single shell field of univalves and bivalves (e.g. Haas, 1981). From the evidence of structure and ontogeny, and discounting the problematic "Pruvot's larva," the existence of this morphocline is seriously questioned.

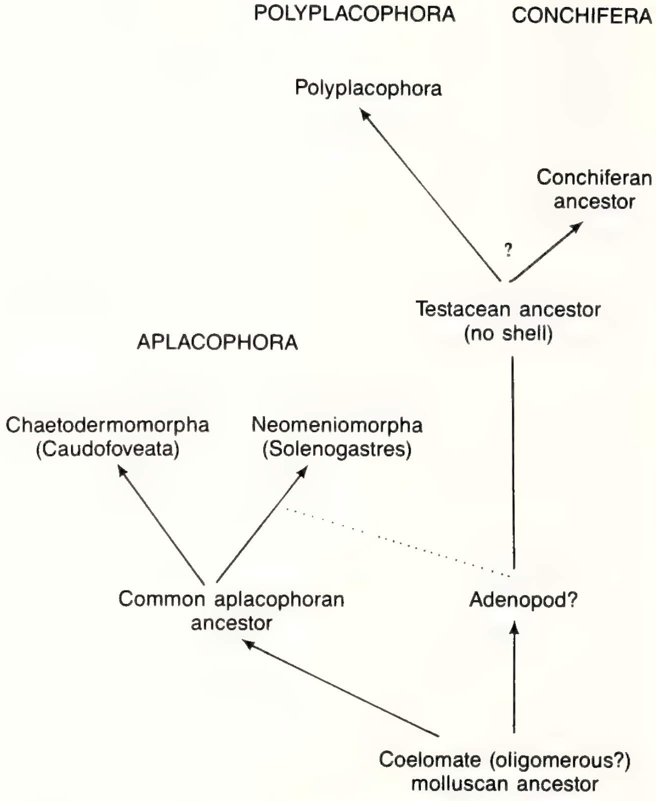
POLYPLACOPHORA
CONCHIFERA
Polyplacophora
Conchiferan ancestor
?
Testacean ancestor (no shell)
APLACOPHORA
Chaetodermomorpha (Caudofoveata)
Neomeniomorpha (Solenogastres)
Common aplacophoran ancestor
Adenopod?
Coelomate (oligomerous?) molluscan ancestor

Fig. 14. Phylogeny of the Mollusca (adapted from Wingstrand, 1985). The questioned Adenopod can be dropped (see argument in section "Chaetoderm oral shield and the archimollusk"). The text raises questions about a common testacean ancestor in comparing chiton and conchiferan shell formation and structure (see argument in section "Shell and Spicules"). A coelomate molluscan ancestor, whether or not oligomerous, is corroborated here (see section "Pericardium"). A common aplacophoran ancestor descended directly from the stem mollusk is indicated (see sections "Chaetoderm oral shield and the archimollusk" and "Aplacophora, a monophyletic group"). The stem mollusk had a paired radula with a two-part radular membrane and distichous teeth (see section "Radula").

Is there a single ancestor for polyplacophorans and the remaining shelled mollusks? Wingstrand (1985) makes a strong case for such a hypothetical testacean ancestor, equivalent to the archiplacophoran of figure 1, based on synapomorphies of radula with its supports and musculature, oral flaps, digestive system, pharyngeal diverticula, 8 pairs of pedal retractors, and, possibly, the number and position of atria (Fig. 13). The shells in chitons are considered to be autapomorphies, but the shell fields and the mineralization process are homologous and monophyletic in chitons and Conchifera. Reasons have been stated above (section on Shell and Spicules) for doubting this homology (Fig. 14). Answers to questions about Pruvot's larva and the relationship of polyplacophoran plates to conchiferan shells could lie in the unknown embryology of *Neopilina* and with the yet-to-be reexamined Pruvot's larva.

RADULA

The direction of evolutionary change in the structure of the aplacophoran radula appears to be from a paired, or bipartite, radular membrane to a single, unipartite ribbon. The rationale for this polarity is based on several points. (1) Rasping seems a more advanced, complicated function for a radula over a simple ability to grasp as found in most Aplacophora. Rasping probably requires the integration of structure provided by a unipartite radular membrane. Only among the Prochaetodermatidae is there wear of the anterior teeth, i.e. evidence of rasping (Scheltema, 1981, 1985), and here the radular membrane is also unipartite. (2) All other radulate aplacophorans except the Dondersiidae and Chaetodermatide with reduced and specialized teeth (Fig. 11; Scheltema, 1972) have a bipartite radular membrane with a fused, unipartite section that often retains visible evidence of fusion; the region of this fused section is not fixed but varies among families and genera (Scheltema, 1981). It is possible, but not parsimonious, to imagine that the radular membrane was originally unipartite, then divided into two, and finally fused again; however, if so, the odontoblasts producing such a secondarily derived, paired radula would have to evolve from a single into a paired group of cells. (3) During ontogeny of the radula in chitons and gastropods, the central tooth is added only after several rows of one or more pairs of lateral teeth have been formed. Presumably the median part of the ribbon is where an originally paired ribbon became unified; subsequently odontoblasts for the central tooth could come into being.

The paired structure of the aplacophoran radula is considered to be the primitive form in mollusks because the direction of evolution, distichous bipartite to distichous unipartite in Aplacophora, is continued in the ontogeny of the gastropod radula, from distichous unipartite to polystichous. Since aplacophorans probably evolved from a shell-less ancestor (see above), the distinctive molluscan structure of a radula was already present when shell evolved (Fig. 14). The aplacophoran plesiomorphic bipartite radula does not form a basis for linking the Aplacophora closely to any other taxon of mollusks.

APLACOPHORA, A MONOPHYLETIC GROUP

The Aplacophora should not be separated into two classes or subphyla on the erroneous homology of the chaetoderm oral shield with a turbellariomorph creeping sole. The oral shield is an autapomorphy of the Chaetodermomorpha. The Neomeniomorpha and Chaetodermomorpha form a monophyletic group with the following probable synapomorphies: a rounded worm shape; a dorsoterminal sensory organ [a chemoreceptor lying external to the mantle cavity, and not known to be ontogenetically or functionally homologous to the osphradium within the mantle cavity of other mollusks (Haszprunar, 1987)]; three to six pairs of precerebral ganglia or swellings (Salvini-Plawen, 1978, 1985); a reproductive system in which the gonads empty into the pericardium through gonopericardial ducts and the pericardium is emptied into the cloaca through coelomoducts (Fig. 13A) (but see Salvini-Plawen, 1972, 1985). An adenopod ancestor becomes a superfluous construct (Fig. 14). As the direction of evolution of organ systems within the Aplacophora becomes clear, new insights into the evolution of mollusks should come to light.

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THE GILLS OF CHITONS (POLYPLACOPHORA) AND THEIR SIGNIFICANCE IN MOLLUSCAN PHYLOGENY

W. D. RUSSELL-HUNTER
DEPARTMENT OF BIOLOGY, SYRACUSE UNIVERSITY,
SYRACUSE, NEW YORK 13244, U. S. A.
and
MARINE BIOLOGICAL LABORATORY
WOODS HOLE, MASSACHUSETTS 02543, U. S. A.

ABSTRACT

It was demonstrated in 1965 that gills of chitons are not paired structures but are added during growth and can show asymmetry. More recent studies, largely on living *Chaetopleura apiculata* (Say) at Woods Hole, confirm the broad homologies of each chiton gill with the aspidobranch ctenidium retained in several stocks of Archaeogastropoda. In particular, similar organization is found of afferent and efferent blood vessels in the gill axis; of alternating ctenidial leaflets; and of lateral, frontal, and abfrontal cilia. In addition to like ciliary functions, both the gastropod aspidobranch gill and each individual chiton gill show similar neuromuscular reflexes in cleansing mucus-bound sediment. One difference, due to the functional organization of each row of chiton gills into a pallial curtain dividing the mantle groove, is the occurrence of Velcro-like ciliary junctions. Unlike junctions in mytilid and other "filibranch" bivalves, which are modified lateral cilia linking adjacent filaments on the same gill, these ciliary junctions link leaflets on adjacent gills and probably represent modified frontal cilia. The coordinated and dynamic functioning of this ctenidial curtain is emphasized, and it is suggested that the adaptive basis on which chitons evolved a curtain by replicating gills, rather than by elongation of ctenidial parts, results from the dynamic pallial groove (unlike the fixed shapes of pallial cavities in bivalves and shelled gastropods). Otherwise chiton gills, along with those of protobranchiate bivalves and certain archaeogastropods, are little altered from "archetypic" molluscan ctenidia.

All archetypes are speculative, available as temporary models of ancestors to be tested by predictions and retrodictions. However, data on gills and other replicated structures in chitons (like data on *Neopilina*, and on molluscan capacity for degrowth) appear to exclude hypotheses involving true metameric segmentation from models of ancestral molluscs.

The multiplied organ systems found in chitons have to be considered in any discussion of metamerism in primitive molluscs. It was demonstrated several years ago (Russell Hunter and Brown, 1965) that the gills of chitons are not paired structures but are added singly during growth, with the result that several species show asymmetry in ctenidial numbers between the left and right sides of individual chitons. Gills continued to be added in adults to meet increased respiratory needs with growth of live tissue mass, and it was concluded that the rows of ctenidia, and probably the other multiplied structures in chitons, reflect functional replication (Russell Hunter and Brown, 1965) rather than the vestiges of more extensive ancestral segmentation as assumed by Lemche (1959b, 1966). The significant feature of the gill rows in dividing the mantle grooves of chitons into functionally inhalant and exhalant chambers had been elucidated by Yonge (1939), and this also stressed functional rather than vestigial multiplication of the gills. Since the discovery in 1952 of the living monoplacophoran genus, *Neopilina* (Lemche, 1957; Lemche and Wingstrand, 1959), discussion of possible metamerism in primitive molluscs has been revised, and continues into the 1980's. Recent Russian investigators of the multiplied structures of chitons (Minichev and Sirenko, 1984) have again concluded that there is no evidence of annelid-like metamerism in their morphogenesis. In his most recent, and beautifully detailed, account of anatomy in Monoplacophora, Wingstrand (1985) still concludes that in chitons, "an oligomeric repetition, probably 7- or 8-metamerism is present" (p. 87, see also pp. 77-81). Given the currency of such divergent views, it seemed appropriate to use this symposium on the Biology of Polyplacophora to present some more recent observations on the functioning of the gills in living chitons. These studies

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were mostly carried out with *Chaetopleura apiculata* (Say) at Woods Hole.

The material presented here involves not only the functional morphology of individual ctenidia in living chitons, but also their combined dynamics as a gill curtain. Two general aspects will be emphasized. First, each chiton gill is a true ctenidium, structurally and functionally homologous with the aspidobranch gill in certain archaeogastropods and with the more primitive gills of protobranchiate bivalves. In addition to reviewing the integrated ciliary and circulatory functions, new observations are presented on neuromuscular cleansing reflexes common to all these primitive molluscan ctenidia. Secondly, new observations give emphasis to the coordinated functioning of the replicated gills as a ctenidial curtain dividing the inhalant from the exhalant pallial chambers, but conforming dynamically to the changing shape and hydraulics of each pallial groove. Some speculation on this as the likely adaptive basis for gill replication in chitons follows, along with a discussion of these and other multiplied structures of chitons. Finally, the implications of such functional replication are considered in relation to hypotheses on interrelationships among the major classes of molluscs, and on metameric segmentation in models of ancestral molluscs.

MATERIALS AND METHODS

In 1979-80 and again in 1986-87, living specimens of *Chaetopleura apiculata* (Say) were studied at the Marine Biological Laboratory (MBL), Woods Hole. This is the "Common Eastern Chiton" of the Atlantic seaboard of the northeastern United States, and most of the material came from boulders on the Buzzards Bay side of Penzance Point near Woods Hole. Other early observations on gills in living specimens of *Lepidochitona cinerea* (L.) were carried out in 1961-63 in Scotland. Over the years 1961-87, other casual observations on living chitons have been made on *Tonicella marmorea* (Fabricius) and *Acanthochitona crinita* (Pennant) in Scotland, and on *T. rubra* (L.) in Massachusetts and Maine. The only observations on *Lepidopleurus cancellatus* (Sowerby) and *L. asellus* (Gmelin) were on material already fixed.

Most observations were made under dissecting microscope (at magnifications from X7 to X30) using incident lighting, with living chitons crawling inverted under glass slides, or on the convex sides of watch glasses. A few observations utilized a temporary "inverted microscope" arrangement of a dissecting microscope pod to check on water currents in chitons crawling dorsal side up (that is with pallial grooves and their contained ctenidia directed downwards). Elucidation of water and ciliary currents, and mapping of mucous secretion and accumulation, involved the injection of particles into the pallial grooves. Particles used included fine carborundum, carmine, Ankolor scarlet S, and dried milk powder. The three figures are diagrams, admittedly reductionist cartoons, each derived from sets of many sketches. Figure 1 is basically from *Lepidochitona*, and figures 2 and 3 from *Chaetopleura*. Some specimens were preserved after partial narcotization using propylene phenoxetol (for details of this method, see Russell Hunter and Brown, 1965), fixation in 12% formalin in sea water, and storage in 10% glycerol. Temporary microscope mounts were made of individual gills, both living and fixed, for viewing both by incident and by transmitted light.

OBSERVATIONS

GENERAL ARRANGEMENT AND NUMERICAL ASYMMETRY

In chitons, the mantle cavity is in the form of two narrow pallial grooves running between the foot and the broad mantle edge or girdle on each side. Each pallial groove contains a row of gills, the bases of which are attached deep in the groove on the girdle side (Fig. 1). The gill curtain forms a functional division of the pallial groove longitudinally into an inhalant chamber, ventral on the girdle side, and an exhalant chamber placed dorsally and pedally (Fig. 1B). As in all molluscan mantle complexes, the anus along with kidney and genital openings discharge in the exhalant stream. Newly formed ctenidia are at the anterior end of each row (Fig. 1A). As growth continues in adult chitons, ctenidia are added anteriorly, irregularly and independently on each side. However, for any species of chiton, there is always a broad correlation between gill number and adult tissue mass (Russell Hunter and Brown, 1965). Asymmetry in ctenidial numbers between the left and right sides of individual chitons occurs in most chiton species. For populations of four chiton species studied in detail, the percentages of asymmetric individuals were 19.5%, 46.3%, 48.4% and 69% (Russell Hunter and Brown, 1965). In most species the numbers of individual chitons with extra left gills are apparently balanced by the numbers with extra right gills. However, Gowlett-Holmes and Zeidler (1987) have described a new species, *Acanthochitona saundersi,* for which all available specimens have 11 ctenidia on the right side and 10 ctenidia on the left side. Asymmetries of ctenidial numbers have been found in at least fifteen species of chitons, and could well occur in the majority of chiton species (Minichev and Sirenko, 1984; A. M. Jones, pers. comm.).

CTENIDIAL FUNCTIONAL MORPHOLOGY

When the gills of a living chiton are viewed from the ventral side, the free tips are seen to be directed toward the edge of the foot (the inner wall of the pallial groove). The gills bulge convexly toward the observer and their axes are defined by the prominent efferent branchial vessels (Fig. 2, ebv). The other (exhalant) face of each axis contains the narrower afferent branchial vessel. The leaflets, which alternate on either side of the gill axis, are short and wide (almost semicircular in face view, Fig. 3), and their tips are opposed (one to one, or one to two) to the tips of leaflets on the next ctenidium in the row (Fig. 2).

Water is moved dorsally (and pedally) by broad bands of lateral cilia (which are more flagella-like) toward the inner and posteriorly directed exhalant chamber (Fig. 3), in a physiologically efficient counter-flow to the blood circulation (afferent branchial vessel to efferent branchial vessel) within

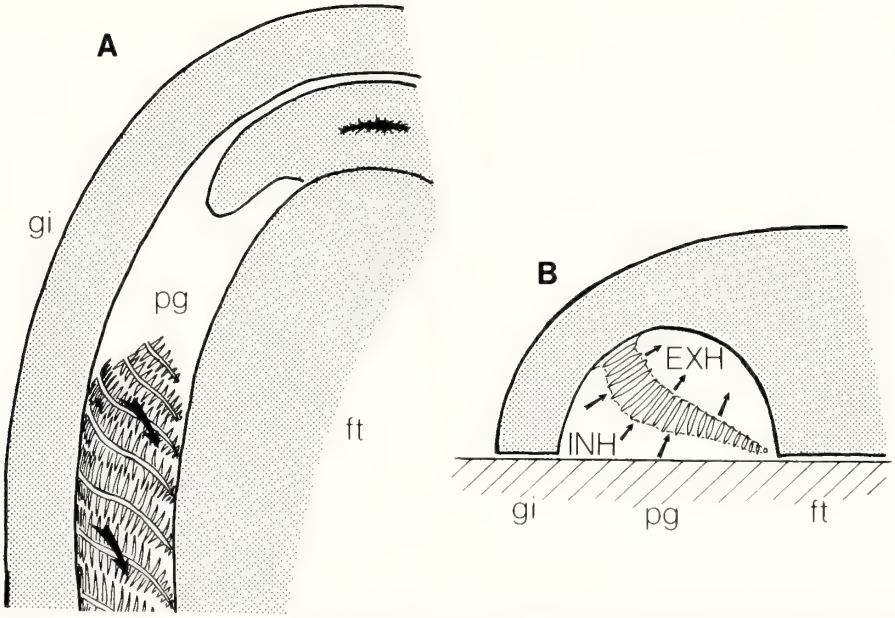

Fig. 1. Diagrams of the mantle groove in a chiton (based on *Lepidochitona*) showing (A) ventral aspect of anterior part of groove, and (B) cross-section of the groove at a central ctenidium. Note that inhalant part of the groove (INH) is girdle-ventral and exhalant part (EXH) is pedal-dorsal (gi, girdle; ft, foot; pg, pallial groove).

each ctenidial leaflet. On the inhalant (INH) side the edges of the leaflets bear shorter frontal cilia (that is, on the facing edges of Fig. 2), and on the exhalant (EXH) side the leaflet edges bear abfrontal cilia. Both frontal and abfrontal cilia have a cleansing (particle-moving) function rather than water propulsion, and transport particles around the leaflet edges toward the axis. The free tips of each leaflet bear specialized longer, less motile cilia that entangle in a Velcro-like fastening (x on Fig. 3) with the corresponding cilia on the leaflet tips of the adjacent ctenidium. From their position, and development in ctenidial buds, these ciliary junctions linking adjacent gills probably represent modified frontal cilia.

The assemblage of microstructures and their functions shown by the chiton gill are thus essentially similar to those found in the primitive "aspidobranch" plume gill of the Archaeogastropoda. If an individual chiton gill is specifically compared with the single plume gill in the limpet, *Acmaea testudinalis* (Müller), the only significant difference involves the Velcro-like ciliary junctions on the chiton leaflet tips. There are obviously minor differences of microanatomy such as the outline proportions of the leaflets, and the distribution of lateral cilia on the leaflet faces, but these seem trivial in comparison with the broader concert of structures and functions. The gill axes with alternating leaflets are essentially identical in arrangement, as are the dorsal afferent branchial vessel and the ventral efferent vessel carrying oxgenated blood back to the heart. The lateral, frontal and abfrontal cilia are arranged in the same way and, in both, the lateral cilia produce a flow of water through the gill (and through the mantle cavity) in the opposite direction to the blood flow. Chiton gills are true ctenidia, structurally and functionally homologous with those of other molluscs. The rows of chiton gills are clearly not neomorphic structures, secondary respiratory organs as in some marine limpets like *Patella*, or in various groups of freshwater pulmonate snails (Russell-Hunter, 1978; McMahon, 1983), but have to be regarded as rows of multiplied ctenidia.

CTENIDIAL CLEANSING REFLEX

Surprisingly little attention has been paid to the muscular movements of primitive molluscan ctenidia. A relatively new set of observations on chiton gills concerns the fact that each ctenidium can move in a patterned cleansing reflex. To anticipate a little, the sequence of movements in the individual chiton ctenidium seems to be exactly similar to that in the cleansing "flick" of the single plume gill in forms like *Acmaea*.

In the axis of the chiton ctenidium, longitudinal muscle fibers lie around and below the two major blood vessels. When both sets of muscle strands contract together, the gill is shortened and pulled toward its base, with a consequent decrease in the gill's contained blood volume. Gill retraction of this sort can be accomplished in 0.2 to 0.8 seconds. Re-extension of the gill is always slower (several seconds) with blood being passed in hydraulically by action of distant antagonists. If the muscle under the afferent branchial vessel alone contracts (stretching the muscle on the efferent side) then the gill curls up into the pallial groove, the ctenidial tip moving away from the foot (Figs. 1, 2). In the opposite case, if the muscle under the efferent branchial vessel contracts the whole gill is straightened and its tip could hit the foot edge or the substratum-surface or both.

If the cleansing cilia (frontal) are experimentally loaded by introducing material (suitably dense but small, like fine grade carborundum) onto the inhalant face of the gill, the foreign particles become mucous-bound and are moved

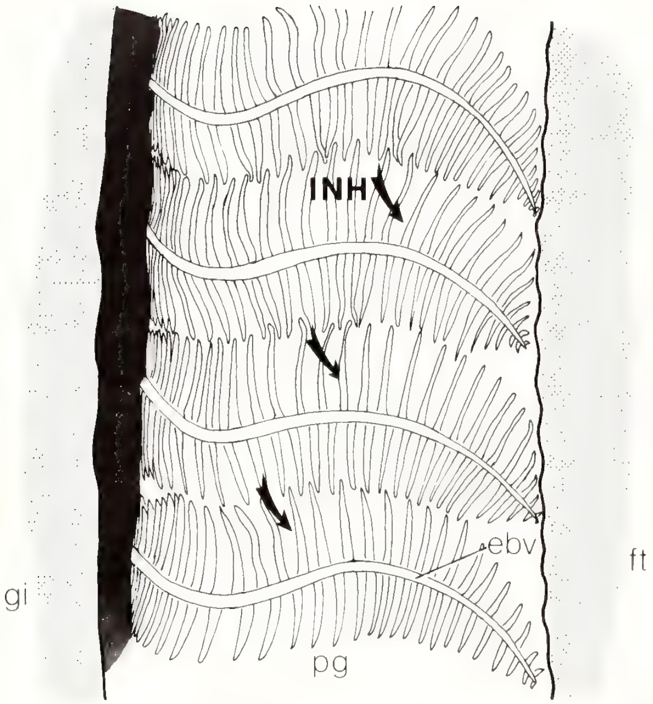

Fig. 2. Diagrammatic view of four ctenidia in *Chaetopleura* from the ventral inhalant side (INH). The axes show the efferent branchial vessels (ebv), and there are frontal cilia on the facing edges of the leaflets. Note that the tips of leaflets are opposed one to one, or one to two (INH, inhalant current; gi, girdle; ft, foot; pg, pallial groove).

toward the axial ciliary tract (Fig. 3) and thence toward the gill tip. In a healthy chiton, accumulation of this sort at the tip provokes a reflex action sequence. The reflex is not gravity dependent and can be observed in chitons in all postural relations to the horizontal. The same reflex takes place if foreign material is loaded on the abfrontal (exhalant) face of the gill. The patterned cleansing reflex occurs in three sequential phases. First, for two to three seconds, more blood is pushed in while the gill expands. (It is difficult to measure this, but the overall volume increase at this phase is usually between 20% and 50%). Secondly, the muscle strands under the afferent branchial vessel contract relatively slowly, taking between 2 and 5 seconds. Thirdly, the muscle under the efferent branchial vessel contracts relatively rapidly, taking between 0.1 and 0.2 seconds, and flicks the tip toward the foot and substratum-surface while simultaneously shortening the gill. (Only at this stage is the contained blood volume reduced again.) In most cases a mucous-bound pellet of natural sediment, or foreign particles, leaves the gill surface and remains on the cilia of the pedal edge or on the substratum. It should be noted that there is never any question of ciliary junctions being formed (even temporarily) between the gill tip cilia and the pedal cilia.

Despite the subtle differences in ctenidial proportions noted above, this reflex action of the individual chiton gill (acting, it seems, in a neuromuscular sense as a peripheral reflex, or almost as an independent effector system) involves a patterned sequence exactly following that observed in the aspidobranch gill of *Acmaea*. Parenthetically, it is worth noting one somewhat special case observed in living chitons, concerning the last large gill in *Chaetopleura*. On several occasions it has been observed to "flick" material right out of the pallial groove, with its tip passing under the girdle in a temporary (and asymmetric) lifting more like the usual local arching of the girdle for typical temporary inhalant openings. Of course, this can only occur because of the distinctly different siting of that last large gill, with its tip directed posteriorly and girdlewards instead of toward the midline and foot. In this respect as others, conditions in the lepidopleurid chitons must be quite different, but we lack observations of living gill movements. In typically near-holobranch chitons like *Chaetopleura* and *Lepidochitona*, groups of three or more ctenidia can flick together. This leads to the second group of new observations.

THE COORDINATED CTENIDIAL CURTAIN

Even the casual observer of the underside of a living chiton can see (Fig. 2) the functional organization of each row of chiton gills into a pallial curtain dividing the mantle groove along most of its length into inhalant and exhalant chambers. This is functionally dependent upon the occurrence of Velcro-like ciliary fastenings on the leaflet tips of chiton gills. Unlike the ciliary junctions in mytilid and other "filibranch" bivalves which are modified lateral cilia linking adjacent filaments on the same ctenidium, these ciliary junctions in chitons link leaflets on adjacent gills and probably represent modified frontal cilia. If the filibranch gills typical of mussels, scallops or oysters are disturbed mechanically, the ctenidial filaments become tangled and the coordinated filtering and sorting functions are temporarily lost. Given otherwise healthy conditions and a little time (usually only a few minutes), the filaments will "crawl" by ciliary action over each other until the appropriate ciliary junctions are reconnected and the seemingly continuous corrugated lamella re-established as a porous water-propelling and filtering surface. Similar processes occur if the ctenidial curtain is mechanically disturbed in a healthy chiton. Individual gills can carry out slower flicks across the pallial groove, but the main re-establishment of the curtain involves the ctenidial tips being "walked" (largely by ciliary action) along the side and edge of the foot, and over each other until an orderly row is again set up. With re-establishment of the row, the ciliary junctions reconnect the tip of one posterior leaflet either to one or to two anterior leaflets on the gill behind it.

In healthy chitons, the way in which each ctenidial row moves as a single dynamic curtain is impressive. It bulges and flattens to accommodate changes in the hydraulics of the pallial groove resulting from shifts in the inhalant (and less frequently the exhalant) openings across the girdle as the chiton crawls along. The early observation of Yonge (1939) that inhalant openings can be formed by local lifting of the girdle at almost any point along the anterior part of the chiton is clearly confirmed. Yonge's conjecture, that the capacity for creating inhalant openings back along the sides of the body is valuable when the anterior end is out of the water, can be supported by the observation that, in *Chaetopleura* at least,

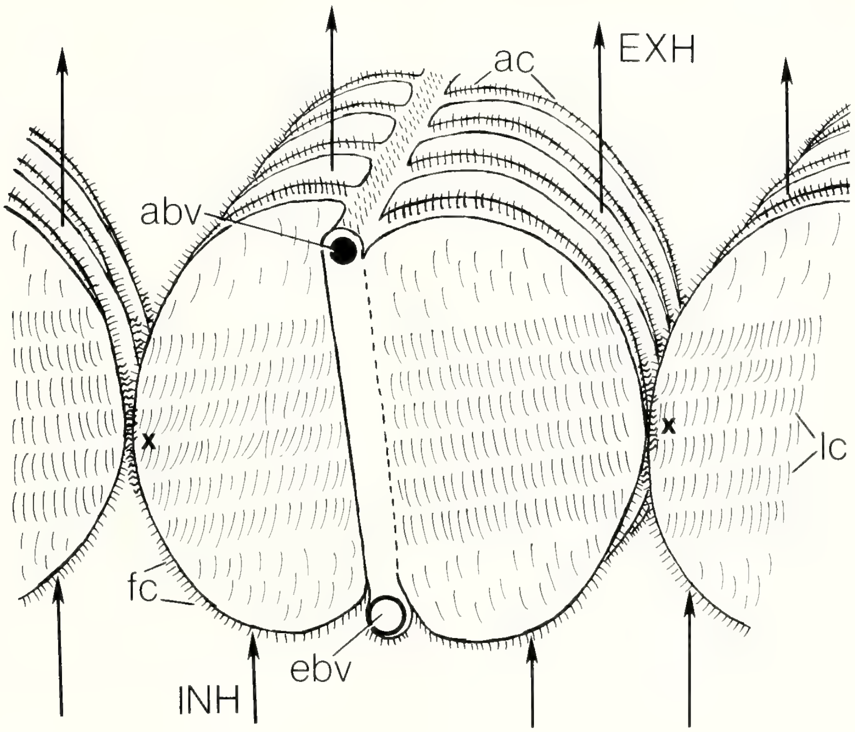

Fig. 3. Stereogram of part of a chiton ctenidium. Water is moved dorsally (and pedally) by bands of lateral cilia (1c). On the inhalant (INH) side, the ctenidial leaflet edges bear front cilia (fc) and the ctenidial axis contains the efferent branchial vessel (ebv). On the exhalant (EXH) side, the leaflet edges bear abfrontal cilia (ac) and the gill axis contains afferent branchial vessel (abv). The opposed free tips of the leaflets bear specialized cilia forming the Velcro-like ciliary junctions (x), probably representing modified frontal cilia.

the continuity of the ctenidial curtain is maintained even with air-bubbles in the anterior third of the groove on both inhalant and exhalant sides of the gill row. Yonge (1939) also noted that the exhalant opening across the girdle was less variable in position, being always at the posterior end. At first sight this seems true in living *Chaetopleura*, and the anus in the midline is always swept by a strong exhalant current. However, while the arching of the girdle to form an exhalant opening always occurs close to the anus, its size (with water velocity inversely related) and its direction (to left or to right of the midline) do vary. As such changes occur, accommodation of the ctenidial curtain to pressure shifts involves it becoming less convex (more flattened towards the foot, decreasing the exhalant cavity volume) or more convex (decreasing the inhalant fraction of the pallial cavity). Changes resulting from shifts in size or direction of the exhalant opening can be particularly obvious in a chiton crawling over a curved or irregular surface. Once again, the simplest set-up used to view a chiton through a flat glass surface can be deceptive.

Working with both living specimens and models of mopaliid chitons, R. S. Cox and his colleagues have applied water flow visualization techniques in flow tanks and have noted muscular contractions of the pallial groove walls (Douglas J. Eernisse, pers. comm.). They have had only equivocal evidence of pallial shape producing augmentation of flow (such as ramming or Bernoulli effects), but my observations suggest that the chiton's ability to modify the exhalant (downstream) pressure by changes in the effective diameter of its exhalant girdle opening could have some significance in shifting the fluid dynamics of the pallial system. Despite this, basic water propulsion and consequent differential pressures in the pallial compartments must all result from the activity of the lateral cilia on the ctenidial leaflets. It is noteworthy that, even in adult chitons, there are always some bands of ciliated epithelia on the walls of the pallial groove which beat in a posterior direction (particularly on the inside of the girdle). Such ciliation is obvious in young (30-day) postlarval chitons, where it exists before the first ctenidial buds and creates analogous water currents (Russell Hunter and Brown, 1965). However, in adults these cilia seem to propel superficial strings of mucus rather than the ambient water.

Despite the adjustments of walls and openings, the dynamic continuity of the ctenidial curtain is maintained as the living chiton crawls along. The direction of the gill axes, with their obvious efferent branchial vessels (Fig. 2), can be seen to be altered but adjacent axes always stay more or less parallel. Groups of six to eight (or occasionally more) gills move together, with their gill-tips lagging behind the foot as the chiton crawls forward, or making a fast recovery so that the gill-tips are seen to be moving forward relative to the edge of the foot. Similarly, groups of ctenidia acting together can move their tips toward and away from the pedal edge. This must involve neural coordination in, for example, the simultaneous contraction of the afferent muscle strands in eight adjacent gills. Some part of the continuity of the curtain could be passive after the ciliary junctions have been connected, but there are obviously also active movements involving the coordination of several ctenidia or even most of the ctenidial row. The ctenidial curtain sometimes shows a metachronal wave of forward movement independent of the foot, or a group of tips crawling together along the foot. Again the loose or temporary attachment of ctenidial tips to the pedal edge does not include any Velcro-like action, although mucous-bound packages of cleansed material are often passed to the foot. In addition, it was already noted that groups of three or more gills could be simultaneously involved in the faster cleansing reflex.

ADAPTIVE SIGNIFICANCE OF THE GILL CURTAIN

Perhaps the most important observation to be made about the whole mantle groove system in chitons is that it is dynamic. Unlike the pallial cavity of a bivalve or shelled gastropod with its relatively static dimensions and shape, the chiton pallial groove is a chamber bounded by pedal and girdle walls whose shapes continually change with movements of the chiton. The chamber wall provided by the habitat surface (Fig. 1B) can also change markedly, since chitons can and do crawl round corners and over edges. Thus the ctenidial curtain has to conform (as a continuous, water-pumping, porous partition) not only to the inhalant and exhalant imposed pressure changes noted above but also to the shape changes of the whole groove system. This is probably the reason why chitons have evolved their pallial curtain by replication of a series of gills rather than by the elongation of axes or of filaments (leaflets) in one pair (or two pairs) of ctenidia. Leaving aside consideration of the evolution of the higher lamellibranch bivalves, the potential for hypertrophy of single units of molluscan ctenidia is amply demonstrated in certain gastropods. In Calyptraeid prosobranchs, a water-propulsive ctenidial curtain is achieved by the elongation into filaments of the leaflets of a single pectinibranch (one-sided) gill. It is proposed that an adaptive functional explanation for the evolution of ctenidial replication in chitons is provided by the dynamic nature of the mantle grooves in the group.

Admittedly, there are two obvious omissions in this survey of the functioning of the ctenidial curtain in chitons. First, there are almost no comparative data on gill function in chitons with Lepidopleurid and other patterns of posterior gills. Although many (perhaps most) species of chitons have long gill rows essentially like those in *Chaetopleura, Lepidochitona* and *Tonicella*, a variety of other conditions have been described. Early workers, such as Pelseneer (1897), developed a syntagma, or array of holobranch and merobranch forms, with metamacrobranchs and mesomacrobranchs, and with or without adanales. A simpler, and probably more functionally significant, classification of certain gill position characters has been utilized by D. J. Eernisse (pers. comm.) in the course of revising the probable higher-level phylogenetic relationships among chitons. Even the most skeptical approach to the use of pallial cavity structures in chiton classification has to separate the Lepidopleurids. Again it would be helpful to know something of comparative gill function in these forms, as well as something of comparative development (Minichev and Sirenko, 1984).

Recent studies on variation in larger population samples of common European chitons (A. M. Jones, pers. comm.) have emphasized the need for a population approach to assessing taxonomic characters. Even in *Chaetopleura*, usually described as holobranch, two distinct forms occur within the populations studied at Woods Hole (Russell Hunter and Brown, 1965) differing in the extent to which each pallial groove is occupied by the ctenidial row. In one form the bases of the gills extend forward for only about 75% of the pallial groove, while in the other the bases extend anteriorly as far as the head fold, and thus conform to the accepted species diagnosis. It is possible that these could reflect phenotypic growth responses to levels of microhabitat oxygenation, but D. J. Eernisse (pers. comm.) has pointed out that, given the lack of knowledge of these stocks, subsequent investigation of other character states might well establish the two forms as separate subspecies or even species. However, none of the new observations presented in this paper would be invalidated if it were subsequently proven that the studied specimens of *Chaetopleura apiculata* from near Woods Hole belonged in two distinct but congeneric species.

The second gap in this presentation on the functioning of the ctenidial curtain in chitons involves the lack of any studies on the ultrastructure of the cilia concerned (particularly those of the ciliary junctions). Any interested investigator with access to SEM facilities, and appropriate techniques of narcotization and fixation, could elucidate much of interest.

SUMMARY OF OBSERVATIONS

Even with these two major omissions, the observations on gills in living chitons can be summarized as five topics. First, the gills are not paired structures but can be added asymmetrically during continued adult growth. Secondly, each gill appears to be structurally and functionally homologous with the aspidobranch ctenidium of archaeogastropods. Thirdly, a neuromuscular cleansing reflex is common to the gills of both chitons and archaeogastropods. Fourthly, each of the two gill rows in chitons is organized as a coordinated ctenidial curtain utilizing ciliary junctions. Fifthly, the adaptive significance of ctenidial replication in chitons (rather than hypertrophy of single units) could lie in the dynamic nature of the pallial space.

DISCUSSION

Many aspects of the phylogeny of molluscs, and of molluscan ancestry, remain controversial. The observations presented here on the gills of living chitons have significance only in relation to two of these aspects: first, the structural and functional homologies of ctenidia and, secondly, the possible metamerism of ancestral molluscs. They can contribute little or nothing to other debates in molluscan phylogeny, such as whether the primitive mantle-cavity was a pallial groove surrounding the head-foot or a posterior cavity with a complex of paired pallial structures, or if the primitive mantle was dome-shaped and secreted a one-piece shell. Similarly, questions of the relationships between the three major classes of "modern" molluscs and the Aplacophora, Monoplacophora and Polyplacophora are barely glossed by this work. The two pertinent questions of ctenidial homologies and of ancestral metamerism both merit further discussion, but the former can be dealt with more simply and its near enthymeme is set out first. Ancestral metamerism requires both some conceptual history and more extensive and multilateral exposition, and these will follow.

In evolutionary hypotheses, organ structures are considered homologous in two or more animal forms if they can be claimed as being derived from a common precursor organ structure in a common ancestral animal (Mayr, 1969, 1983; Russell-Hunter, 1979). Such theoretical claims are normally based on similarity of fundamental structural plan in the organs concerned, on similar anatomical associations with other organs, and on similarities in their embryonic development. Since such claims are inferential, most modern evolutionists would prefer them to be phrased in terms of maximum likelihood. When, as in the case of the molluscan pallial cavity and ctenidium, we have a whole concert of organs and functions operating in an integrated fashion, there is likely to exist what can be termed functional homology (Russell-Hunter, 1968, 1979). It can be deduced that extensive patterns of functional interdependence must be encoded by largish packets of integrated genetic material commonly derived (since the precursor animal must also have been an efficient machine with similar functional interdependence). Cytogenetic levels of linkage need not be postulated. On the other hand, attempts at the enumeration of discrete unit characters for the molluscan ctenidium and its associated pallial complex for either cladistic (Hennig, 1950, 1966) or phenetic analysis would be relatively uninformative from such an integrated system (Mayr, 1974, 1983). The ctenidium, a gill with characteristic patterns of ciliated epithelia and blood vessels, is found as a homologous structure in Gastropoda, Bivalvia, and Cephalopoda (Yonge, 1947).

In each mollusc with them, the ctenidia are part of an integrated functional system: the heart and other blood vessels, certain glands and sense-organs, the external openings of genital and renal systems, and the posterior part of the alimentary canal are all structurally and functionally stereotyped in their relationships to the ctenidia. As pointed out elsewhere (Russell-Hunter, 1968, 1979), it is highly significant that, although probably at least 75,000 molluscan species (out of about 110,000) have ctenidia, and although there are many aquatic animals belonging to other phyla which seemingly could make good use of a ctenidium, no nonmolluscan animal has one. The above observations on gills in living chitons can only confirm the conclusion reached by Yonge (1939, 1947) that the gill rows represent multiplied ctenidia. David R. Lindberg (pers. comm.) remains unconvinced of homology between gills of chitons and those of gastropods, largely on the basis of differences between the two classes in the blood vessels draining the haemocoelic spaces of the body and supplying the afferent branchial vessels of the gills. However, it is not the preafferent circulation that links the ctenidium with its associated pericardial and pallial structures in a functionally homologous complex, but the postefferent connections to the auricles, auriculoventricular openings, and the rest that do so. Further, there is considerable variation within gastropods in the arrangement of the preafferent vessels. The attempt by Lemche (see especially Lemche, 1966) to suggest that bivalves and cephalopods have gills of different origin from those of gastropods was based on a misunderstanding of the relationships of their suspensory ligaments in respect to the branchial vessels. It was associated with his claims for homology between the gills of chitons and those of *Neopilina* (Lemche, 1959a, 1966) and, in turn, between the gills of *Neopilina* and the limbs of arthropods like trilobites (Lemche, 1959b, 1966). Each chiton gill is a true ctenidium, structurally and functionally homologous with the aspidobranch gills of Archaeogastropoda and the protobranch gills of more primitive Bivalvia. Again, it has to be admitted that this concluding hypothesis of homology for chiton gills makes little contribution to the vexed questions of further homology with the gills of *Neopilina* (Lemche, 1966) or with the gills in certain Aplacophora (Scheltema, 1973, 1988).

The other phylogenetic controversy, that on metameric segmentation in the ancestral mollusc, is less easy to set forth. Before attempting to outline its history and arguments, some statement of premises regarding both metameric segmentation and archetypes as models of ancestors may be appropriate. The essence of metameric segmentation as found in annelids and arthropods is the serial succession of segments each containing unit-subdivisions of the several organ systems (Hyman 1951; Russell-Hunter, 1968, 1979). The sequence of morphogenesis of these segments is anteroposterior from a penultimate budding zone, so that the segments just behind the head are older, and the more posterior ones (just in front of the budding zone) are younger. The differentiation of additional segments in this mode of morphogenesis is such that each new segment contains (at least initially or potentially) a full set of all organ systems.

Archetypes are not ancestors. For any stock of animals, the characteristics of the actual ancestral forms will never be known with certainty. Archetypes are logical constructs, temporary models set up from reductionist explanations of available data, to be tested by the collection of further data. The testing can invalidate, but can never authenticate (despite the current belief of certain systematists that their cladistic hypotheses can be confirmed by separately computed phenetic analyses). When considering such models, in view of what Mayr (1983) terms "cohesion of the genotype", it seems particularly important to consider possible functional homologies as well as the more usual morphological ones (Russell-Hunter, 1979). Significant functional unity is apparent within each phylum of more complex animals (including molluscs, arthropods, echinoderms, and chordates). There are obvious pragmatic values in setting up ancestral models. There are peculiar dangers in evolutionary discussions after setting up an archetype, and these seem to result from assembling together in the unfortunate hypothetical animal a group of incompatible structures, all thought to be "primitive" or "plesiomorphic" within the stock. As noted elsewhere (Russell-Hunter, 1968, 1979), many of these dangers can be avoided if, when a hypothetical ancestral type is constructed, an attempt is made to create a working archetype — one in which the concert of organs and functions could operate as a whole, in an integrated functional plan, as in all living organisms. In discussing similar matters in the adaptive morphology of vertebrates, Bock (1965) (see also Bock and von Wahlert, 1965) has clearly stated the need for analyses of function in the whole animal. The working archetype (Russell-Hunter, 1968, 1979) can be set up from a deduced concert of structures and functions together forming an integrated functional plan, and can then provide a better basis for phylogenetic speculation and both predictive and retrodictive testing.

Molluscan archetypes with short segmented bodies had been proposed by Pelseneer (1899, 1906) and Naef (1926), largely on the basis of studies on the genital and excretory systems of chitons and cephalopods. However, the extensive and convincing work of the molluscan functional morphologists such as Yonge, Graham and Fretter on ciliary mechanisms, ctenidial blood vessels, and renopericardial and genital ducts (particularly in more primitive gastropods) set up a very different model for the stem-mollusc. As set out in fecund summary by Yonge (1947), although primitively bilaterally symmetrical, this archetype was totally unsegmented and possessed a posterior mantle-cavity enclosing a pallial complex of paired structures which included two ctenidia. This model convincingly survived retrodictive testing against the fossil record, as clearly set out by Knight (1952) who was able to fit appropriate pallial circulation and muscle attachments into the lower palaeozoic monoplacophoran genera, *Scenella* and *Pilina*, regarded then as untorted "pregastropods." Pragmatically, it is important to note that versions of Yonge's model are still employed in the 1980's by systematists (Salvini-Plawen, 1980; Seed, 1983) and pedagogues (Russell-Hunter, 1979, 1982) both as gastropod archetype and as bivalve archetype and, as regards the paired pallial structures and homologous ctenidia of these two stocks, have survived much testing.

Discussion of possible metamerism in ancestral molluscs was reopened by the discovery of a living monoplacophoran, *Neopilina*, by its preliminary description (Lemche, 1957) and by the extensive description of its morphology (Lemche and Wingstrand, 1959) that followed. It was hypothesized that the mollusc ancestor must have shown relatively complete metamerism, that this is present to a somewhat reduced extent in *Neopilina*, that this is still further reduced in chitons, and that this metamerism degenerates so completely as to be undetectable in gastropods and bivalves (Lemche and Wingstrand, 1959). Subsequently Lemche (1966) reversed part of this hypothesis and claimed that the arthropods originated directly from a molluscan ancestor. For a few years, many strange phylogenies were based on *Neopilina* as a "missing link" rather than as an interesting survivor of a less successful molluscan stock. In this respect, the claims of homology among the gills of chitons, the gills of *Neopilina*, and the arthropod limbs of trilobites (Lemche 1959b, 1966) begin to approach the idealist metabiological comparisons of William Patten. As noted elsewhere (Russell-Hunter, 1985), Patten's use, early in this century of detailed comparative anatomy to postulate an origin of vertebrates in arachnids (or merostomatids like *Limulus*), represents a comparatively late derivative of the *Naturphilosophen* of Johann Wolfgang von Goethe (1749-1832), and is perhaps closest in concept to the publications of Lorenz Oken in the first half of the nineteenth century. Even without idealist morphology, in the work of Lemche and Wingstrand (1959) on *Neopilina*, and in the beautiful reconstructions subsequently presented by Wingstrand (1985), it is explicit that the multiplied organs of chitons (shells-valves, muscles, gills and nerves) reflect metameric segmentation. Indeed, after detailed comparisons of *Neopilina, Vema* and chitons, Wingstrand (1985) concludes that a homologous 8-metamerism is present in the Polyplacophora. Such a chiton archetype with true metamerism can be tested appropriately with the data on actual replicated structures in chitons including the numbers and symmetry of gills (Russell Hunter and Brown, 1965), and the functioning of the gill series (this paper). Even when the other multiplied structures are considered, there is little of the serial succession of segments, each with unit subdivisions of organ systems, in any living chiton, and there is no evidence of serial organogenesis. The mantle rudiment of a settled postlarval chiton secretes six plates. After an interval a larger anterior plate is added then, still later, a small posterior plate. There is never a budding zone as in the annelid-arthropod mode of development. Segmentation in heart structures is even less valid. Chitons all have an elongate ventricle in the midline which receives blood from two symmetrical elongate auricles. Most chitons have two pairs of auriculoventricular openings, several genera have one pair, and chiton species are known with three pairs and with four pairs. Both *Neopilina* and *Nautilus* have four auricles and therefore also have two pairs of auriculoventricular openings. Individual ctenidia in chitons cannot be related to any other replicated organs, such as shell-valves, nephridial lobes, lateropedal nerve connections or heart structures, and thus cannot be allocated to specific metameric segments. Other features of chiton gills and their functioning complete this negation of the metameric archetype for chitons. The gills are not paired but are added asymmetrically during continued adult growth. As individual gills, they seem to be structurally and functionally homologous with those of primitive bivalves. This replication in chitons results in gill rows, which show coordinated function as pallial curtains and cannot reflect simplification of more extensive metamerism. Ctenidial replication in chitons can be claimed to result adaptively from the dynamic nature of the pallial grooves in the chiton body form.

Similar arguments can be used to criticize the concept of annelid-arthropod metamerism applied to the described structures of *Neopilina* and *Vema*. This statement should not be taken as critical of the majority of the interesting homologies elucidated by Wingstrand (1985), in particular his meticulously exhibited parallels between chitons and the two monoplacophoran genera not only in pedal retractor muscles but also in the muscles of the buccal mass and radula. However, living monoplacophorans have five (or six) pairs of gills, eight pairs of pedal retractor muscles, two pairs of auricles, six (or seven) pairs of nephridiopores, two (or three) pairs of gonads, and a single shell (Wingstrand, 1985). This assemblage is unlikely to have arisen by segmental morphogenesis.

In his claims for molluscan metamerism, Wingstrand (1985) appears to rely on the concept of a monophyletic Protostomia or Spiralia, linked by common features of early cleavage, gut development and larval type. It may be best to quote his own words (Wingstrand, 1985: 89): "The metamerism of molluscs is in itself hardly unexpected, for many features support their incorporation within the Spiralia, a group in which different kinds of metameric repetition are common." Unfortunately, the concept of a group of phyla forming the Spiralia is itself suspect. The five diagnostic features used to discriminate the group from the Deuterostomia are neither so universal nor so consistent as to justify a clear dichotomy (Russell-Hunter, 1979). Larval homologies have been in doubt since Garstang (1922, 1929) seriously challenged recapitulation as an important factor in the evolution of larval stages. Cleavage is a dynamic process in time and spiral cleavage is not absolutely correlated with mosaic development. As Costello (1948, 1955) pointed out, there are three main categories of cleavage (radial, bilateral and spiral), and three basic types of spiral cleavage (by quartets, by duets and by monets), but all are modified into bilateral cleavage later in development. He emphasized that the occurrence of spiral cleavage has no obvious significance in the interrelationships of animal phyla (Costello and Henley, 1976).

There is another kind of developmental evidence linking molluscs and flatworms and making molluscan metamerism less likely. Recent work on actuarial bioenergetics has emphasized the capacity for degrowth in some shelled molluscs (Russell-Hunter *et al.*, 1983, 1984; Russell-Hunter, 1985), and compared it in flatworms. Along with other features of indeterminate growth, many gastropods and bivalves show a capacity to degrow (as individuals to reduce the mass of their structural proteins under certain circumstances), no close-coupling of growth with sexual maturation, and a lack of endogenous senescence (Russell-Hunter and Eversole, 1976; Russell-Hunter and Buckley, 1983; Russell-Hunter, 1985). It has been hypothesized (Russell-Hunter, 1985) that this capacity in flatworms and molluscs could involve controls of genetic expression that cannot coexist with those involved in a metameric pattern of morphogenesis. Some molecular biologists studying ageing indicate accumulated errors in the synthesis of macromolecules as important (Kirkwood, 1977; Kirkwood and Holliday, 1979), and they correlate the absence of endogenous senescence in certain organisms with indeterminate growth patterns. The neurohormonal and hormonal controls for metameric development may mandate selective gene-expression in some irrevocable fashion that is incompatible with cellular dedifferentiation-rejuvenation, and with the capacity of degrowth exhibited by molluscs and flatworms. This hypothesis of incongruent controls of morphogenesis in molluscs and in metamerically segmented animals cannot yet be tested experimentally. That it can be proposed illustrates the weight of circumstantial evidence that metameric organogenesis of the sort which produces serial sets of structures in the phyla Annelida and Arthropoda never occurs in the Mollusca.

As already admitted, conditions in the stem-mollusc remain controversial. The general conclusion from the present work that chitons do not show true metameric segmentation seems established at a high level of likelihood. Extending the logic, evidences against metamerism of the annelid-arthropod pattern in all primitive molluscs are strong, and a consensus with the views of Wingstrand and of Salvini-Plawen could be achieved if their protoannelid ancestor for the molluscan stock were totally without metameric segmentation, indeed if it were an unsegmented flatworm turned coelomate. All model ancestors are highly speculative.

At the end of the earlier paper on chiton gills (Russell Hunter and Brown, 1965), an archetype mollusc with a four-fold basic organization (that is, with four ctenidia, four auricles, four renal organs, etc.) was proposed. This derived from a footnote query by C. F. A. Pantin in Yonge (1947), and reflected the heart morphology of *Neopilina, Nautilus* and chitons. Somewhat surprisingly, this model is mentioned favorably not only by Minichev and Sirenko (1984) but also in passing by Wingstrand (1985). From such a four-fold organization, two sorts of subsequent morphogenesis could occur. Both a line of organisms with one gill on either side, and a line with many, could thus evolve from an archetype with two pairs of gills. In this hypothesis, the former stock (that is, those with one pair of ctenidia, one pair of auricles, one pair of renal organs, and so on) could still be regarded as archetypic for the two major groups of living molluscs: the gastropods and the bivalves. But, as reiterated pedantically here and elsewhere, archetypes are not ancestors.

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A REVIEW OF CARIBBEAN ACANTHOCHITONIDAE (MOLLUSCA: POLYPLACOPHORA) WITH DESCRIPTIONS OF SIX NEW SPECIES OF *ACANTHOCHITONA* GRAY, 1821

WILLIAM G. LYONS
FLORIDA DEPARTMENT OF NATURAL RESOURCES
ST. PETERSBURG, FLORIDA 33701, U. S. A.

ABSTRACT

Nine previously described species of Acanthochitonidae are recognized in the region between Bermuda and the Caribbean coast of South America: *Acanthochitona andersoni* Watters, 1981; *A. astrigera* (Reeve, 1847); *A. balesae* Abbott, 1954 (+*A. elongata* and *A. interfissa*, both Kaas, 1972); *A. bonairensis* Kaas, 1972; *A. hemphilli* (Pilsbry, 1893); *A. pygmaea* (Pilsbry, 1893); *A. rhodea* (Pilsbry, 1893); *Choneplax lata* (Guilding, 1829); *Cryptoconchus floridanus* (Dall, 1889). Four new species (*Acanthochitona lineata, A. roseojugum, A. worsfoldi,* and *A. zebra*) are described from Florida, the Bahama Islands and the northern Caribbean; *Acanthochitona venezuelana sp. nov.* is described from Margarita Id., Venezuela; *Acanthochitona ferreirai sp. nov.* is described from Pacific coasts of Panama and Costa Rica. No subsequently collected specimens were seen of *Acanthochitona spiculosa* (Reeve, 1847), originally described from the West Indies; *A. spiculosa* is considered a *species inquirenda*.

Until recently, seven species of Acanthochitonidae generally were recognized in the Caribbean region (Bermuda, Florida, and the Bahama Islands to the north coast of South America): *Acanthochitona spiculosa* (Reeve, 1847) [+*A. astriger* (Reeve, 1847)]; *A. hemphilli* (Pilsbry, 1893); *A. pygmaea* (Pilsbry, 1893); *A. rhodea* (Pilsbry, 1893); *A. balesae* 'Pilsbry' Abbott, 1954; *Choneplax lata* (Guilding, 1829); *Cryptoconchus floridanus* (Dall, 1889). In 1972, P. Kaas published a monograph on the Polyplacophora of the Caribbean region. In his treatment of Cryptoplacidae (=Acanthochitonidae), Kaas (1972) proposed *A. elongata* to replace *A. balesae* 'Pilsbry', recognized as valid the other six species, and described two new species, *A. bonairensis* and *A. interfissa*, increasing to nine the number recognized from the region. Kaas was followed by G. T. Watters' (1981) review of New World *Acanthochitona*, in which he declared *A. astriger* to be separate from *A. spiculosa*, assigned *A. pygmaea* to the synonymy of *A. spiculosa*, assigned *A. rhodea* to the synonymy of *A. hemphilli*, resurrected *A. balesae* Abbott, with synonyms *A. elongata* and *A. interfissa*, declared *A. bonairensis* to be a synonym of the European *A. communis* (Risso, 1826), and described a new species, *A. andersoni*. As a result, the number of recognized Caribbean species of Acanthochitonidae was reduced to eight.

In a report on the Polyplacophora of Barbados published four years later, A. J. Ferreira (1985) proposed additional changes in the classification of Caribbean Acanthochitonidae. Ferreira recognized *Acanthochitona astrigera, A. spiculosa, A. bonairensis,* and *Cryptoconchus floridanus*, reversed Watters' action by assigning *A. hemphilli* to the synonymy of *A. rhodea*, and declared *A. andersoni, A. balesae,* and *A. interfissa* to be juveniles, and thus synonyms, of *Choneplax lata*. Six recognized species of Caribbean Acanthochitonidae remained.

In this report, I present new conclusions based upon examination of type specimens of *Acanthochitona andersoni, A. astrigera, A. bonairensis, A. hemphilli, A. interfissa, A. pygmaea, A. rhodea,* and *A. spiculosa*. I have relied extensively on specimens in the collection of the Florida Department of Natural Resources (FDNR) and in the research collection of Dr. R. C. Bullock, University of Rhode Island. I also re-examined many museum specimens utilized previously by Kaas (1972), Watters (1981), and Ferreira (1985). After Dr. Ferreira's death in 1986, his collection was transferred to the California Academy of Sciences. Unfortunately, only the dry collection could be inspected during 1987.

Nine previously named species and five new species of Acanthochitonidae that occur in the Caribbean region are described and illustrated. Relationships between Caribbean species and their eastern Pacific cognate species are discussed, and one eastern Pacific cognate species is described as new.

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METHODS

Complete species treatments should provide full descriptions and illustrations of valves, spicules and radulae. Examinations of spicules and radulae of taxa treated here are still in progress and so cannot be presented. Instead, this report presents conclusions derived principally from characters of the valves, with less emphasis on girdle spicules and no information on radulae. Descriptions, illustrations, and differential diagnostic comments are provided for all of the species. Characters described include general dimensions, color, shape of the jugum, tegmentum, sutural laminae, and insertion plates, tegmental pustule morphology, and counts and measurements of girdle spicules. Species are illustrated with SEM photographs of valves and tegmental pustules as well as with photographs of intact specimens.

Tegmental pustules are illustrated in near-perpendicular aspect from anterolateral portions of left or right sides of intermediate valves, depending upon specimen condition. As shown in illustrations of entire valves, pustules usually are arranged in rows parallel to the jugum, but individual pustules are aligned anterolaterally, so pustular apices point posterolaterally toward the jugum.

Longitudinal lines or incisions on the jugum are mentioned often in descriptions of *Acanthochitona*. In fact, lines are visible within the jugum of nearly all species examined, but lines at the surface are uncommon. Careful examination in most instances reveals that such lines are internal and do not interrupt the jugal surface. Whether the surface is smooth or incised can be ascertained by using scanning electron microscopy or, with light microscopy, by using high magnification with light directed obliquely at a low angle across the short axis of the jugum.

Measurements of small intact specimens, individual valves, and girdle spicules were made using a Zeiss IV-B dissecting microscope with ocular micrometer. Dimensions of tegmental pustules were measured from scanning electron micrographs of known magnification. Large intact specimens were measured with vernier calipers. Most specimens were flat when preserved, so measurements are accurate to 0.1 mm. Lengths of slightly curled specimens were determined by making several incremental linear measurements along the longitudinal curve; those lengths are accurate to about 0.5 mm. Extremely curled specimens were not measured. Data presented for individual species lots include number of specimens, size range (total length), location, depth, date of collection, and museum catalogue number.

Specimens were examined from or deposited in the following institutional collections: Academy of Natural Sciences of Philadelphia, Pennsylvania (ANSP); British Museum (Natural History), London [BM(NH)]; California Academy of Sciences, San Francisco (CAS); Delaware Museum of Natural History, Wilmington (DMNH); Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg (FSBC I); Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution, Ft. Pierce, Florida (IRCZM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Tulane University Department of Geology, New Orleans (TUDG); and the National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM).

SYSTEMATIC ACCOUNTS

Family Acanthochitonidae Pilsbry, 1893
Genus *Acanthochitona* Gray, 1821
Acanthochitona hemphilli (Pilsbry, 1893)

Figs. 1-9

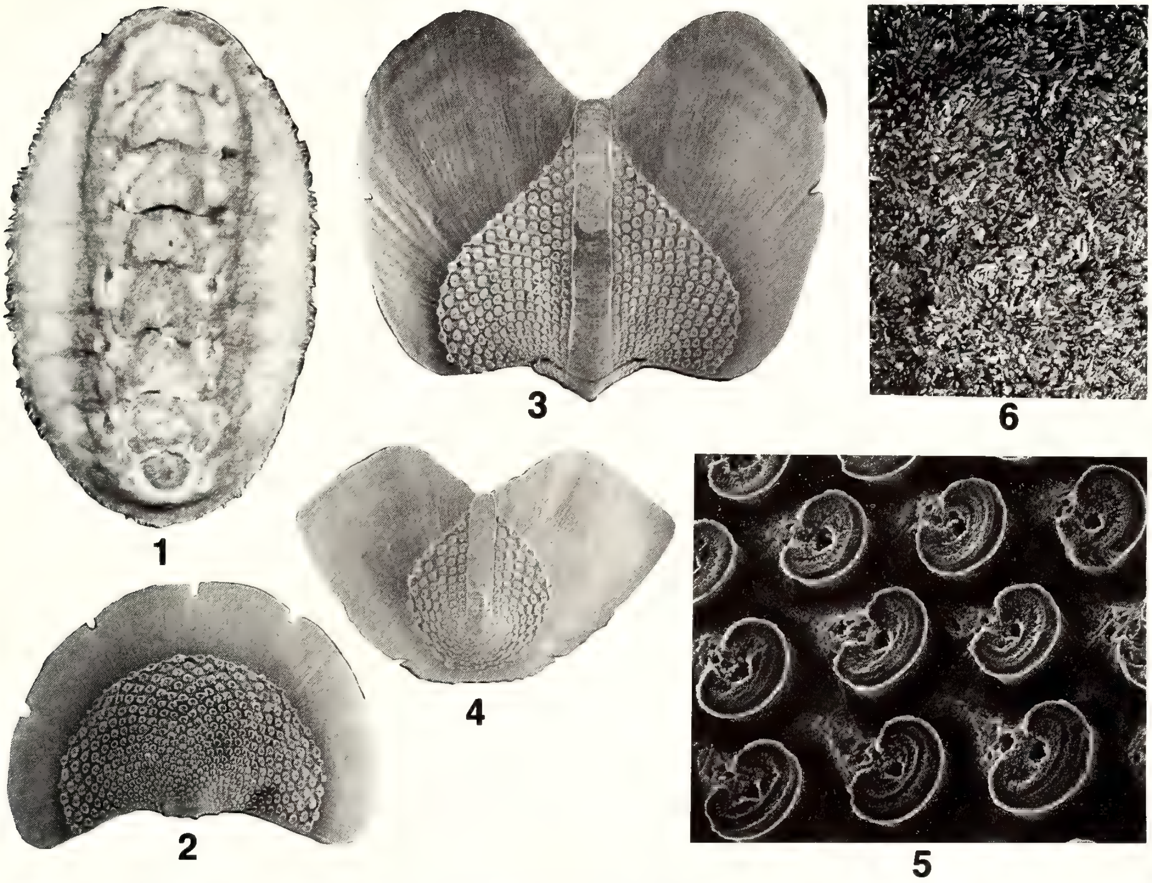
Acanthochites (Notoplax) hemphilli Pilsbry, 1893: 34, 35, pl. 13, figs. 65-67.
Acanthochitona hemphilli, Kaas, 1972: 38-41, figs. 58-64, pl. 2, figs. 1, 2 (pars). Watters, 1981: 173 (pars).
Acanthochitona rhodea, Ferreira, 1985: 207, 208 (pars) [*non A. rhodea* (Pilsbry, 1893)].

TYPE MATERIAL: LECTOTYPE: ≈ 24 mm, partially disarticulated; Key West; ANSP 35803 (herein designated).

OTHER MATERIAL EXAMINED: FLORIDA: 3 spec., 33.4-34.5 mm, Long Key Reef, Dry Tortugas, intertidal, 11-12 May 1979, FSBC I 32042. —1 spec., 13.0 mm, patch reef near Long Key Reef, 1.5-2.5 m, 11 May 1979, FSBC I 32428. —2 spec., 33.5, 38.4 mm, Bird Key Reef, Dry Tortugas, 0.5-1.0 m, 4 Oct 1979, FSBC I 32044. —8 spec., 23.8-44.2 mm, Garden Key, Dry Tortugas, 1-2 m, 13 May 1979, FSBC I 32043. —6 spec., 15.2-44.1 mm, Garden Key, 0-2 m, 5 Oct 1979, FSBC I 32045. —1 spec., 29.3 mm, Sand Key off Key West, 0.5-2.0 m, 3 Aug 1980, FSBC I 32046. —2 spec., 30.0-36.2 mm, Western Sambo Reef off Key West, 4.2-7.3 m, 12-21 Mar 1973, FSBC I 9397. —1 spec., 50.9 mm, off Pompano Beach, southeast Florida, 18.3 m, 1981, FSBC I 32429. BAHAMAS: 27 spec., 10.0-51.3 mm, Bahama Beach Canal, West End, Grand Bahama, intertidal, 29 Aug 1984, FSBC I 32049. —5 valves, Gold Rock, Grand Bahama, bottom sediments, 24.4 m, May-July 1981, FSBC I 32519. —14 spec., 8.0-37.5 mm, McLeanstown, east end Grand Bahama, 1-2 m, 24 May 1981, FSBC I 32047. —19 spec., 4.5-47.0 mm, McLeanstown, 1 m, 27 Aug 1984, FSBC I 32048. —8 valves, Grand Bahama, bottom sediments, May 1981, R. Quigley collection. —11 spec., 30.5-47.6 mm, Harbour Id., Eleuthera, 0-3 m, 24 Aug 1978, FSBC I 32041. —3 spec., 23.8-41.9 mm, Fernandez Bay, Cat Island, 3 m, 10-16 July 1976, FSBC I 15804. —1 spec., curled, Georgetown, Great Exuma, 0-1 m, 21 June 1974, FSBC I 32518. TURKS AND CAICOS ISLANDS: 8 spec., 11.1-51.3 mm, Providenciales, 0-2 m, 22 Sept 1986, FSBC I 32430. PUERTO RICO: 2 spec., 38.8, 41.6 mm, Cayo Enrique, La Parguera, 0-1 m, 19 Aug 1985, FSBC I 32050. —8 spec., 15.2-32.1 mm, Magueyes Id., La Parguera, 20 Apr 1966, Bullock collection. JAMAICA: 1 spec., 30.8 mm, 3 km west of Runaway Bay, 0-1.5 m, 3 Nov 1983, Bullock collection. CAYMAN ISLANDS: 1 spec., 35.8 mm, Grand Cayman, 1965, FSBC I 5549. BELIZE: 2 spec., curled, Carrie Bow Cay, 8 m, 21-24 Oct 1973, FSBC I 10765. —8 spec., curled, Carrie Bow Cay, 23 Mar 1981, IRCZM 61:050. HONDURAS: 2 spec., 22.6, 34.5 mm, Anthonys Key, Roatan, 4-10 July 1971, Bullock collection. —13 spec., all curled, Oak Ridge, Roatan, intertidal, Mar 1987, FSBC I 32431. —5 spec., 24.0-32.1 mm, Roatan, 1981, FSBC I 32520.

TYPE LOCALITY: Key West, Florida (original designation).

DISTRIBUTION: South Florida and Grand Bahama Island to Puerto Rico, Jamaica, and Honduras; intertidal to 18 m.



Figs. 1-6. *Acanthochitona hemphilli* (Pilsbry, 1893). **Fig. 1.** Whole specimen, 42.6 mm; Harbour Id., Eleuthera, Bahamas; FSBC I 32041. **Fig. 2.** Valve i *ex* 15.2 mm specimen; Dry Tortugas, Florida; FSBC I 32045. **Fig. 3.** Valve iv, same specimen. **Fig. 4.** Valve viii, same specimen. **Fig. 5.** Tegmental pustules, valve v, 16.7 mm specimen; same lot (field width = 330 μm). **Fig. 6.** Spicules of dorsal girdle mat, specimen from McLeanstown, Grand Bahama; FSBC I 32047 (field width = 500 μm).

DESCRIPTION: Largest specimen 51.3 mm long, 28.0 mm wide including girdle; valves occupying about 30% of total specimen width (Fig. 1). Exposed parts of valves dark red with white maculations, small relative to total specimen size; unexposed valve parts greenish white. Girdle broad, fleshy, appearing smooth, dark brown, with few brown or reddish brown spicules in dorsal tufts; color of girdle and tufts sometimes faded in preserved material.

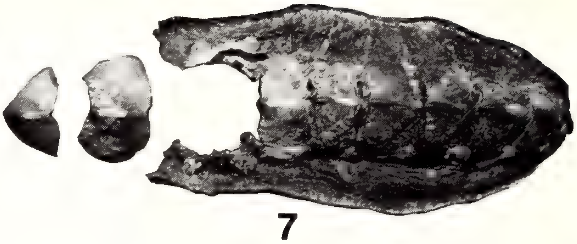
Valve i semilunate (Fig. 2), wider than long, beaked, sinuous posteriorly, with anterior insertion plate bearing 5 slits; tegmentum occupying about 65% total valve length. Valves ii-vii strongly beaked (Fig. 3); tegmentum spade-shaped, about as long as wide, strongly constricted anteriorly, with broadly sinuous anterolateral margins; sutural laminae broad, expanded anteriorly, with subparallel lateral margins rendering overall valve shape nearly quadrate except for broad, shallow anterior sinus; single small narrow slits near midpoints of margins. Valve viii subtriangular (Fig. 4), rounded posteriorly, with elevated mucro posterior of center; tegmentum drop-shaped, longer than wide, constricted anteriorly; sutural laminae large, flared anterolaterally, with straight to sinuous anterior margins, separated by wide V-shaped sinus; 2 slits in posterior insertion plate small, narrow, V-shaped.

Jugum smooth, narrow, with parallel sides well-separated from lateral tegmental surface. Tegmentum of all valves covered with small (35-50 μm), round to ovate, cupped pustules with edges incised at apex to render overall appearance reniform (kidney-shaped) (Fig. 5), with single central macresthete, 2-3 micresthetes.

Girdle upper surface appearing smooth, actually covered with dense mat of very small (50 μm) slender, sharp, brown spicules (Fig. 6); 18 anterior and sutural dorsal tufts with about 50 thick, reddish-brown to white, flat-sided spicules, longest 1.5-2.0 mm; slender, needle-like, sharp spicules interspersed among larger spicules of tufts; margin with dense fringe of straight, slender, brown and white spicules 1.0-1.5 mm long; underside covered with small (50 μm) slender, sharp, white spicules directed toward periphery.

DISCUSSION: *Acanthochites hemphilli* Pilsbry, 1893, was described from a specimen collected at Key West, Florida, and the name generally has been applied to the large ($>$50 mm) fleshy species that occurs in south Florida, the Bahama Islands, and the northern Caribbean Sea. *A. rhodeus*

Pilsbry, 1893, was described from a specimen bearing only the data "Panama (McNeill Expedition)", prompting subsequent question as to whether *A. rhodea* properly belonged to the Caribbean fauna, the eastern Pacific fauna, or perhaps to both. Leloup (1941) reported specimens of *Acanthochiton rhodeus* from off Cabo la Vela, Caribbean Colombia, and provided additional descriptive notes for the species. Keen (1958) listed *Acanthochitona rhodea* in her compendium of mollusks from the eastern Pacific but noted that the species might belong to the Caribbean rather than the Panamic fauna. A. G. Smith (1961) seemed to confirm the presence of *A. rhodea* in the eastern Pacific when he contrasted its characters with those of *A. tabogensis* Smith, 1961, and *A. hirundiniformis (=hirudiniformis)* (Sowerby, 1832), two other species from that region. The name again appeared on a list of Caribbean fauna in Houbrick's (1968) account of species from Costa Rica. Thorpe (*In* Keen, 1971) illustrated a specimen identified as *A. rhodea* and listed its range as Mexico (Pacific Ocean) to Peru. Kaas (1972) summarized descriptions by Pilsbry and by Leloup and treated the species as a member of the Caribbean fauna. The species again was illustrated and reported from Caribbean Colombia by Götting (1973). Watters (1981) relegated *A. rhodea* to the synonymy of *A. hemphilli* without discussion of morphological characters or geographic range, only to be followed soon thereafter by Ferreira (1985) who declared *A. hemphilli* to be a synonym of *A. rhodea*, citing page priority of the original descriptions. Ferreira concluded that the complex constituted a single species ranging from Florida and the Bahamas to Brazil in the western Atlantic Ocean and from Mexico to Peru in the eastern Pacific Ocean. Examination of type-specimens of both species, as well as additional materials from Florida, the Bahama Islands, several localities in the northern Caribbean, the Caribbean coast of Central America, and the Pacific coasts of Costa Rica and Panama, indicates that the complex actually consists of three species, including one previously undescribed.



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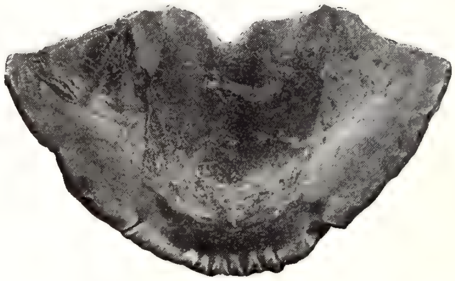

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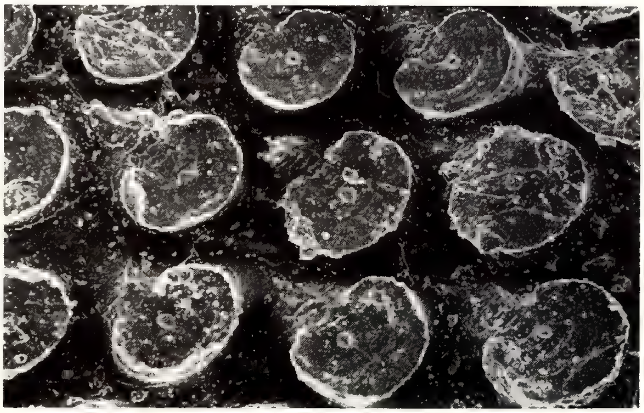

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Figs. 7-9. *Acanthochitona hemphilli* (Pilsbry, 1893), lectotype; Key West, Florida; ANSP 35083. **Fig. 7.** Whole specimen. **Fig. 8.** Valve viii, ventral. **Fig. 9.** Tegmental pustules, valve vii (field width = 345 μm).

One of Pilsbry's specimens (ANSP 35803) is herein designated as lectotype of *Acanthochites hemphilli* Pilsbry, 1893. Pilsbry described a dried specimen 24 mm in length. The lectotype measures about 24 mm overall and is partially disarticulated (Fig. 7); valves i-vi remain attached to the girdle, but valves vii and viii are free. Pilsbry described the posterior valve viii as "...not bilobed behind, having the usual two slits, and between them a number (6-8) of smaller, irregular and unequal slits or nicks". That this is the specimen described by Pilsbry is confirmed by the condition of valve viii, which is aberrant. The valve has two slits in the usual positions (Fig. 8), but one slit is unusually large and wide, whereas the other is unusually small and narrow; the reported irregularities are also present.

Asymmetrical tail valves are not unusual in *Acanthochitona*; several valves viii of *A. astrigera* which I examined were misshapen, some completely lacking one of the posterior slits. All other characters of the lectotype, including the reniform tegmental pustules (Fig. 9), indicate the specimen to be conspecific with material reported here as *A. hemphilli*. The reniform pustules, "smooth" girdle, greenish white sutural laminae, and subquadrate, parallel-sided intermediate valves distinguish *A. hemphilli* from *A. rhodea* and from the new species.

Acanthochitona hemphilli now is demonstrated to occur from southeast Florida and the northern Bahama Islands southward to Puerto Rico, Jamaica, Belize, and Honduras. Specimens reported from Cuba (Jaume and Sarasúa, 1943) and Caribbean Mexico (Vokes and Vokes, 1983) are probably referable to this species, whereas those reported from Caribbean Panama (Olsson and McGinty, 1958) almost certainly are *A. rhodea* (see that species account). Specimens illustrated by Kaas (1972: pl. 2, figs. 1, 2) from Curaçao as *A. hemphilli* are *A. rhodea.* Other reports of *A. hemphilli* from Barbados, Bonaire, and Venezuela (Ferreira, 1985) and Aruba (Kaas, 1972) could also represent *A. rhodea.* Records by Righi (1971) of *A. hemphilli* in Brazil seem especially unlikely because the specimens were collected in 47-115 m depths, far deeper than the 18 m maximum depth otherwise known for the species.

Acanthochitona rhodea (Pilsbry, 1893)

Figs. 10-18

Acanthochites rhodeus Pilsbry, 1893: 26, 27, pl. 12, figs. 48-51.
Acanthochiton rhodeus, Leloup, 1941: 39-42, figs. 5-7.
Acanthochitona rhodea, Keen, 1958: 519 (pars). Kaas, 1972: 42, 43, figs. 65-71. Götting, 1973: 251-253, pl. 11, figs. 15, 16. Bullock, 1974: 164 (pars). Ferreira, 1985: 207, 208 (pars).
Acanthochitona rhodeus, Houbrick, 1968: 10, 20.
Acanthochitona hemphilli, Kaas, 1972: pl. 2, figs. 1, 2 (pars). Watters, 1981: 173 (pars) [*non A. hemphilli* (Pilsbry)].

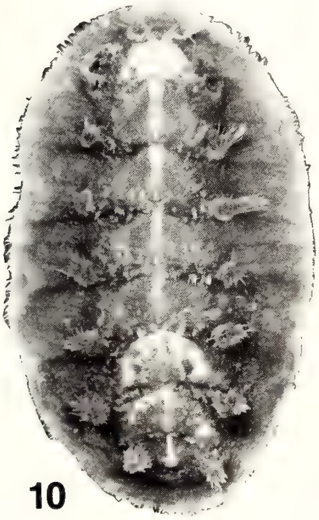
TYPE MATERIAL: HOLOTYPE: 3 disarticulated valves, "Panama; McNeill Exped.", ANSP 63429.

OTHER MATERIAL EXAMINED: COSTA RICA: 2 spec., both curled, Portete, Limon Prov., 12 June 1966, USNM 702874. PANAMA: 1 spec., curled, Toro Point, Ft. Sherman, Canal Zone, Sept 1969, Bullock collection. —4 spec., 6.5-27.0 mm, Ft. Randolph, Canal Zone, 1 m, Nov 1980, FSBC I 32530. —10 spec., 1.8-30.0 mm, Galeta Id., Canal Zone, Bullock collection. —20 spec., 19.7-32.5 mm, Galeta Id., Sept 1973, FSBC I 32562 (1), Bullock collection (19). —2 spec., 10.3, 25.1 mm, near Portobelo, 0-1 m, Nov 1980, FSBC I 32529. —2 spec. 12.0, 12.4 mm, Cocal Point, Portobelo, 13 Sept 1973, Bullock collection. —12 spec., 24.5-39.5 mm, Ironcastle Point, Portobelo, 13 Sept 1973, Bullock collection.

TYPE LOCALITY: Portobelo, Caribbean coast of Panama (by subsequent designation, Ferreira, 1985).

DISTRIBUTION: Caribbean coasts of Costa Rica, Panama, and Colombia; intertidal to 53 m.

DESCRIPTION: Largest specimen slightly curled, 39.5 mm long, 24.0 mm wide including girdle; valves occupying approximately 30% of total specimen width (Fig. 10). Exposed parts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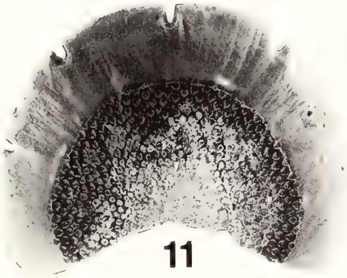
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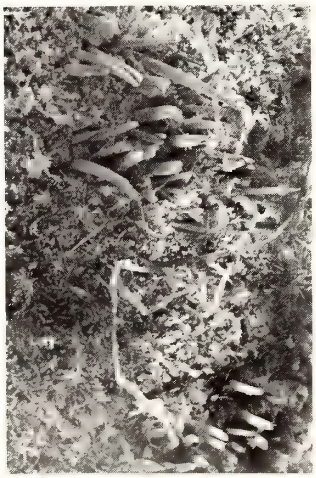
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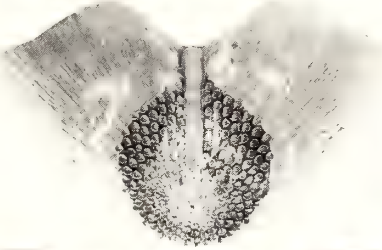
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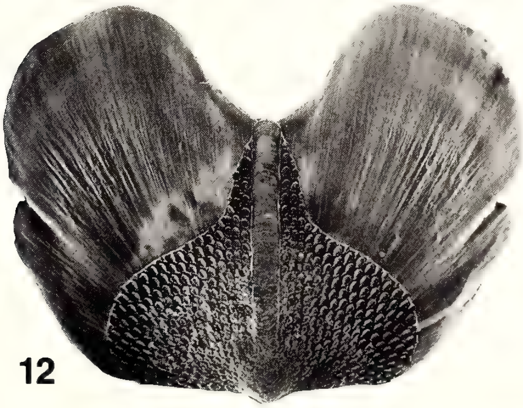
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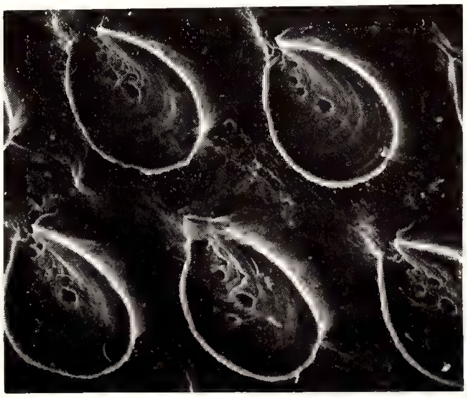
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Figs. 10-15. *Acanthochitona rhodea* (Pilsbry, 1893). **Fig. 10.** Whole specimen, 25.1 mm; Portobelo, Panama; FSBC I 32529. **Fig. 11.** Valve i *ex* 25.0 mm specimen; Galeta Id., Panama; FSBC I 32562. **Fig. 12.** Valve iv, same specimen. **Fig. 13.** Valve viii, same specimen. **Fig. 14.** Tegmental pustules, valve iv, same specimen (field width = 340 μm). **Fig. 15.** Spicule clusters, dorsal girdle mat, same specimen (field width = 550 μm).

of valves dark red with white maculations; unexposed parts dark red to plum. Girdle broad, fleshy, tan to dark reddish brown, appearing smooth but with very small clusters of short, stout, white spicules widely scattered on dorsal surface, especially where girdle intrudes between valves; long spicules in dorsal tufts reddish brown, shorter basal spicules of tufts blue-green.

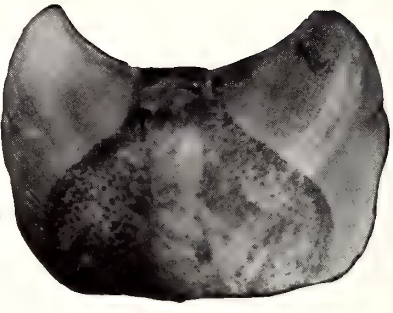
Valve i semilunate (Fig. 11), wider than long, concave posteriorly, with anterior insertion plate bearing 5 U-shaped slits; tegmentum occupying about 65% total valve length. Valves ii-vii beaked (Fig. 12); tegmentum alate (wing-shaped), little wider than long but constricted over much of anterior portion, with markedly concave anterolateral margins; sutural laminae very large, longer than wide, broad, flared anterolaterally, separated anteriorly by wide, deep, U-shaped sinus; lateral margins not parallel to each other or to jugum; single slits near midpoints of margins. Valve viii broadly triangular (Fig. 13), about twice as wide as long, rounded posteriorly, with mucro posterior of center; tegmentum drop-shaped, longer than wide, constricted anteriorly along jugum; sutural laminae very wide, flared anteriorly, separated by wide, V-shaped sinus, with straight anterior margins; 2 slits in posterior insertion plate small, narrow, V-shaped.

Jugum smooth, narrow, with parallel sides well-separated from lateral tegmental surface, extending anteriorly beyond main body of tegmentum. Tegmental pustules drop-shaped (Fig. 14), 120 μm long, 80 μm wide, with single central macresthete, 3-6 micresthetes nearly all adapical of macresthete.

Girdle upper surface covered with dense mat of very small (50 μm) brown spicules interrupted by clusters of stout, white, 200-400 μm long spicules (Fig. 15), clusters very sparse on main dorsal surface, dense where girdle intrudes between valves; 18 anterior and sutural tufts containing about 50 straight, stout, sharp-tipped spicules up to 2 mm long, brown along shafts, blue-green at base, with extremely fine, needle-like spicules within base; margin fringed with slender, straight or slightly curved, sharp-tipped blue or blue-green spicules up to 1.4 mm long; underside densely covered with slender, sharp-tipped spicules about 80 μm long, directed toward periphery.

DISCUSSION: Pilsbry (1983) described *Acanthochitona rhodea* from an alcoholic specimen 28 mm long, 15 mm wide, that had already "lost the cuticle and hairs from its girdle, leaving a smooth whitish surface pitted at the sutures." Thus, one important identification character, the girdle spicules, could not be described. Now all that remains of the holotype are three disarticulated valves, ii, vii(?), and viii (Figs. 16-18). Nevertheless, sufficient evidence remains in the drop-shaped pustules, well-illustrated by Pilsbry (1893: pl. 12, fig. 49), to demonstrate that *A. rhodea* is the species that inhabits the Caribbean coast of Panama. Thus, Ferreira's (1985) restriction of the type locality to Portobelo was appropriate.

Characters important in separating *Acanthochitona rhodea* from *A. hemphilli* include the drop-shaped rather than reniform pustules, the dark red rather than greenish white sutural laminae, and the small clusters of stout spicules widely scattered among the mat of shorter spicules on the dorsal surface of the girdle. Differences between *A. rhodea* and the Pacific coast species are discussed under remarks following the description of that species.



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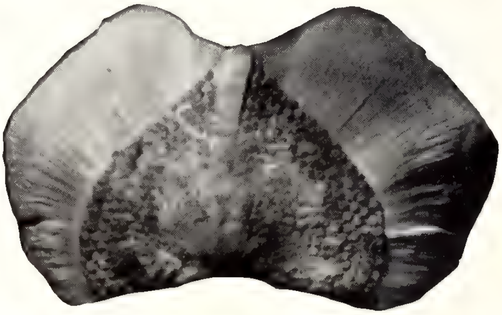

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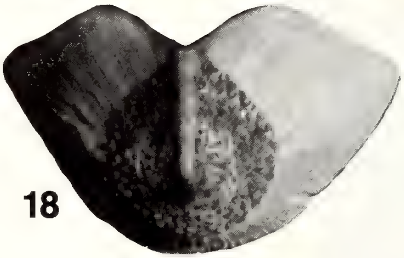

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Figs. 16-18. *Acanthochitona rhodea* (Pilsbry, 1893), holotype; "Panama"; ANSP 63429. **Fig. 16.** Valve ii. **Fig. 17.** Valve vii (?). **Fig. 18.** Valve viii.

Ferreira's (1985) distributional records of *Acanthochitona rhodea* are unreliable because he identifed all three species as *A. rhodea.* Houbrick's (1968) specimens from the Caribbean coast of Costa Rica, which I examined, are *A. rhodea.* Leloup's (1941) description and illustrations of drop-shaped tegmental pustules (his figs. 5, 6) and large spicules scattered in widely separated groups among the smaller spicules of the dorsal girdle surface demonstrate that his specimens from off Colombia in 28-29 fm (51-53 m) were *A. rhodea.* Scattered spicule clusters on the girdle and shapes of valves i, vii, and viii indicate that specimens illustrated as *A. hemphilli* from Curaçao by Kaas (1972) are *A. rhodea.* Likewise, Götting's (1973) illustration of scattered clusters of girdle spicules indicates that specimens he reported as *A. rhodea* from Caribbean Colombia were identified correctly. Thus, the species is known with certainty only from the southern Caribbean Sea, where it usually is collected in the shallow subtidal zone.

Acanthochitona ferreirai Lyons, *sp. nov.*

Figs. 19-24

Acanthochitona rhodea, Keen, 1958: 519, fig. 10 (pars). A. G. Smith, 1961: 89. Thorpe *In* Keen, 1971: 867, 868, fig. 14. Bullock, 1974: 164 (pars). Ferreira, 1985: 207, 208 (pars). [*non A. rhodea* (Pilsbry, 1893)].

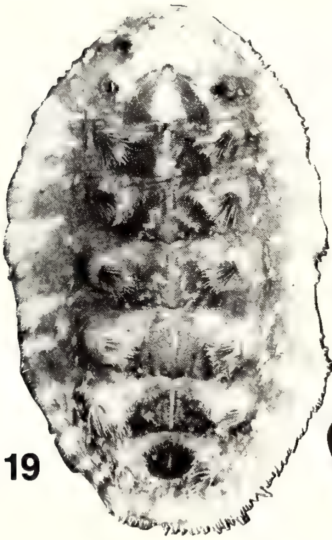
TYPE MATERIAL: HOLOTYPE: 28.2 mm, Punta Mala, Pacific coast of Panama, July 1969, R. C. Bullock, collector, USNM 859314. PARATYPES: PANAMA: 13 spec., 9.4-28.2 mm, collected with holotype, ANSP A12121 (1), CAS 064883 (1), RMNH 55985 (1), FSBC I 32563 (2), Bullock collection (8). COSTA RICA: 2 spec., 19.6, 26.5 mm, Playa de Jaco, intertidal, 25 Apr 1975, FSBC I 32564.

TYPE LOCALITY: Punta Mala, Panama.

DISTRIBUTION: Pacific coasts of Costa Rica and Panama; intertidal and shallow subtidal depths.

DESCRIPTION: Largest specimen (holotype) 28.2 mm long, 17.0 mm wide including girdle; valves occupying approximately 65% of total specimen width (Fig. 19). Exposed valves uniformly red or rose, usually with white maculations; unexposed parts rose pink. Girdle broad, orange-brown or dark red, with large white patches of spicules unevenly spread across dorsal surface; spicules of dorsal tufts green.

Valve i semilunate (Fig. 20), wider than long, concave posteriorly, with anterior insertion plate bearing 5 slits; tegmentum occupying about 65% total valve length. Valves ii-vii beaked (Fig. 21); tegmentum alate, twice as wide as long, constricted anteriorly, with anterolateral margins concave near jugum; sutural laminae broad, flared anterolaterally, separated anteriorly by wide, shallow sinus; lateral margins not parallel with each other or with jugum; single slits near midpoints of margins. Valve viii broadly triangular (Fig. 22), twice as wide as long, rounded posteriorly, with nearly central mucro;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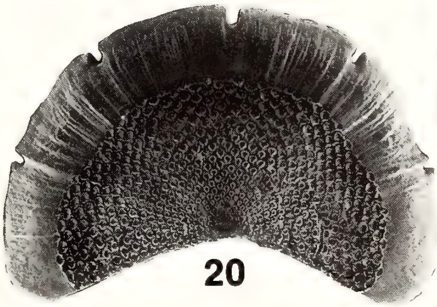
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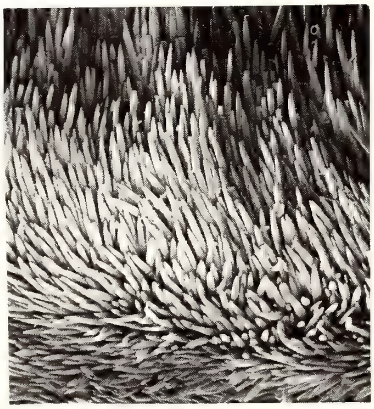
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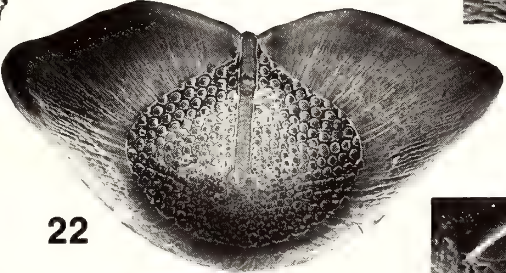
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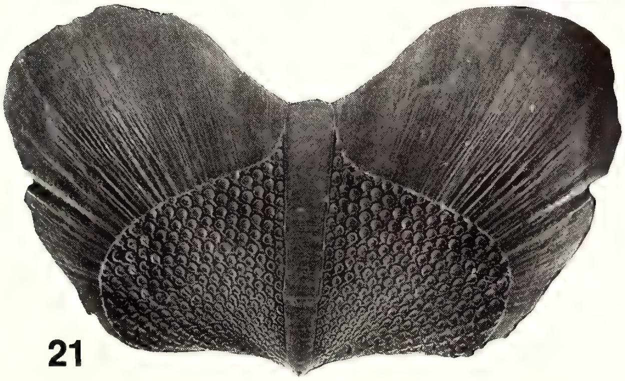
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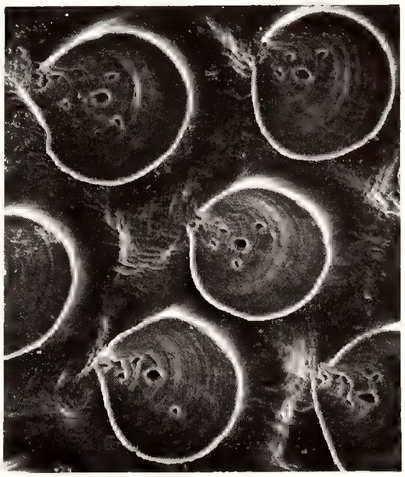
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Figs. 19-24. *Acanthochitona ferreirai* Lyons, *sp. nov.* **Fig. 19.** Holotype, 28.2 mm; Punta Mala, Panama; USNM 859314. **Fig. 20.** Valve i *ex* 24.5 mm paratype; same location; FSBC I 32563. **Fig. 21.** Valve iv, same specimen. **Fig. 22.** Valve viii, same specimen. **Fig. 23.** Tegmental pustules, valve iv, same specimen (field width = 280 μm). **Fig. 24.** Dorsal girdle spicules, same specimen (field width = 650 μm).

tegmentum ovate, wider than long, constricted anteriorly along jugum; sutural laminae very wide, flared anterolaterally, with straight anterior margins, separated by very shallow, broad, V-shaped sinus; 2 slits in posterior insertion plate small, narrow, V-shaped.

Jugum smooth, narrow, with parallel sides well-separated from lateral tegmental surface, extended anteriorly beyond main tegmental mass. Tegmentum of all valves covered with small (100 μm) round to slightly ovate pustules (Fig. 23), with single subcentral macresthete, 3-4 micresthetes.

Girdle upper surface covered with dense mat of very small (60 μm) spicules overlain by extensive patches of slender, straight, white spicules 400-500 μm long (Fig. 24), especially evident posteriorly and where girdle intrudes between valves; 18 anterior and sutural tufts containing 50-60 straight or slightly curved, stout, sharp-tipped green spicules up to 2.2 mm long; margin fringed with slender, sharp-tipped spicules up to 1 mm long, arranged in alternating groups of purple and white; underside densely covered with slender, sharp-tipped spicules about 80-90 μm long, directed toward periphery.

DISCUSSION: *Acanthochitona ferreirai* is related to *A. hemphilli* and, especially, to *A. rhodea* of the Caribbean region. The relatively shorter, wider valves, round to subovate tegmental pustules, and dense, clearly evident patches of longer spicules on the dorsal surface of the girdle separate *A. ferreirai* from the other two species.

This is the species reported from the eastern Pacific as *Acanthochitona rhodea* by Keen (1958), A. G. Smith (1961), Thorpe (*In* Keen, 1971), Bullock (1974), and Ferreira (1985). Together, those authors reported specimens ranging from Mexico to Peru. I examined only specimens from Costa Rica and Panama, so I cannot confirm that specimens from Mexico and Peru are conspecific with the material described here.

ETYMOLOGY: Named for the late Antonio J. Ferreira, whose work stimulated much interest in Caribbean and Panamic polyplacophorans.

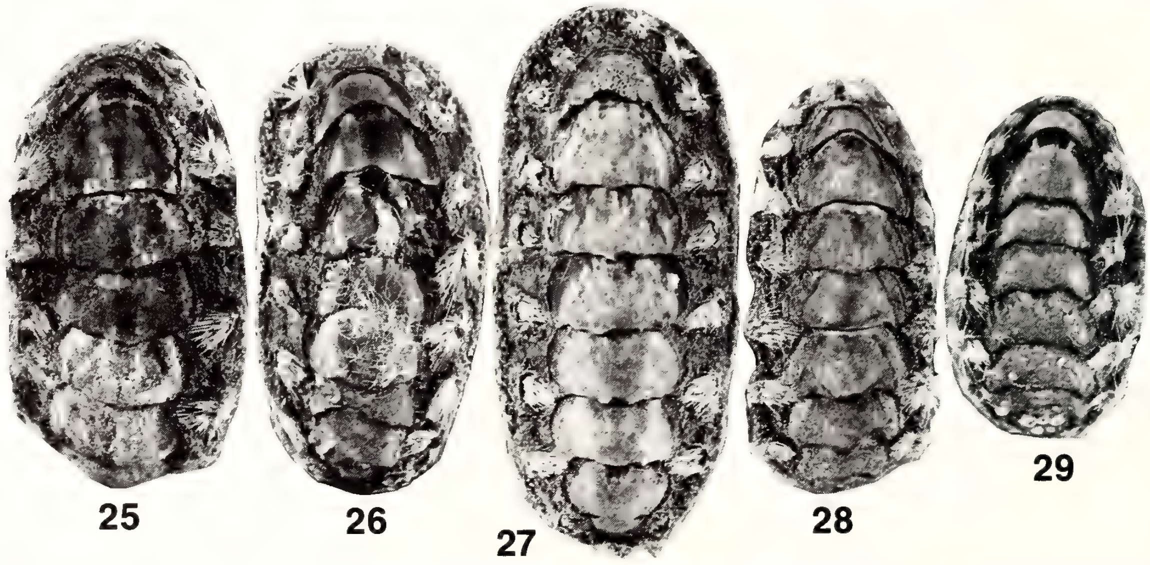
***Acanthochitona spiculosa* (Reeve, 1847)**

Figs. 25-29

Chiton spiculosus Reeve, 1847: pl. 9, sp. and fig. 47.
Acanthochites spiculosus, Pilsbry, 1893: 22, pl. 13, figs. 60-62.
(*non Acanthochitona spiculosa* of subsequent authors).

TYPE MATERIAL: LECTOTYPE: 33.0 mm; "Loc. West Indies; Cuming collection; Acc. 1829"; BM (NH) 1981251/1 (herein designated). PARALECTOTYPES: 4 spec., 21.0-28.0 mm; collected with lectotype; BM (NH) 1981251/2-5.

DISCUSSION: All five types (Figs. 25-29) at one time were glued to a tablet by either the dorsal or ventral surface. Three specimens contain the dried remains of the foot and viscera, and two have been scraped clean beneath. Within one of the latter, a tag was glued but has been removed, leaving only a torn remnant upon which no information remains. This specimen [BM(NH) 1981251/1], previously labeled as the figured syntype, is the most flattened and best preserved of the specimens and most resembles Reeve's figure 47 in its proportions of length and width; it is designated herein as the lectotype. However, if this is the specimen figured by Reeve, considerable liberties were taken to enhance the illustration. Reeve's figure depicts a black, smooth, shiny surface over all valves; each intermediate valve is drawn with a distinct jugal separation extending obliquely from the posterior beak to the anterolateral corners of the exposed valve surface; a single concentric band appears near the lateral margins of each valve. Spicules of dorsal tufts are depicted as long, densely packed, and fully spread from each cluster, overlying the entire girdle and extending beyond its narrow margin. The



Figs. 25-29. *Acanthochitona spiculosa* (Reeve, 1847), type specimens, "West Indies". **Fig. 25.** Paralectotype, 27.0 mm; BM(NH) 1981251/3. **Fig. 26.** Paralectotype, 28.0 mm; BM(NH) 1981251/2. **Fig. 27.** Lectotype, 33.0 mm; BM(NH) 1981251/1. **Figs. 28, 29.** Paralectotypes, 26.0, 21.0 mm; BM(NH) 1981251/4, 5.

spicules are olive with traces of blue-green.

The actual syntypes are not nearly so attractive. Expectedly, having been dried for more than 150 years, the girdles are shrunken and hardened, and many of the spicules are broken. However, the greatest difference between the specimens and Reeve's description is in the condition of the dorsal tegmentum. The jugal tract and most of the lateropleural areas of each valve of every specimen are severely eroded, evidently as a result of surf abrasion (this condition occurs frequently among Caribbean species such as *Acanthopleura granulata, Chiton squamosus,* and *Ceratozona squalida* which inhabit intertidal zones of surf-swept rocks). The only remaining tegmentum occurs near lateral margins of the valves; the intersection of original tegmentum and eroded valve is evidently the concentric band depicted in Reeve's figure. On some specimens, the jugal area is marked by an eroded dark band set apart by lighter areas at each side, but the only actual remnants of jugum were found beneath the overhang of the posterior edge of the preceding valve on valve ii of the smallest curled specimen and on valve viii of the next larger curled specimen. The jugum is black, nearly smooth but microscopically pitted. No incisions are evident on the jugum of any syntype. The densely arranged pustules near lateral margins of intermediate valves are so coated with grime that their form is difficult to discern, but, where apparent, they vary from ovate to drop-shaped.

Four types of spicules occur on the girdle. Those of the 18 dorsal tufts, although frequently broken, are most evident, being long, round, sharp-pointed, and densely packed; individual lengths vary considerably, as do corresponding thicknesses; their color is now light golden brown. Aside from the tufts, the dorsal surface of the girdle is covered with short, blunt-tipped, club-shaped brown spicules. Fairly short, slender, vitreous, sharp-pointed spicules form a fringe at the outer margin of the girdle. On the underside, densely packed, very short, vitreous spicules barely break the girdle surface. Particles of quartz sand occur among debris trapped in girdle spicules of the types.

The taxonomic history of *Acanthochitona spiculosa* has been greatly confused. Much of that confusion can be traced to W. H. Dall and E. A. Smith. Dall (1889a) identified as *A. spiculosa* specimens hereafter shown to be *A. pygmaea* (Pilsbry, 1893). In the following year, E. A. Smith (1890) combined *A. spiculosa* with *A. astrigera* (Reeve, 1847). Pilsbry (1893) included *A. spiculosa* among species in the West Indian fauna, but he only attempted to reproduce Reeve's description verbally and visually and did not report any additional material. A full synonymy of correct and incorrect applications of the name *A. spiculosa*, and of its confusion with *A. astrigera, A. pygmaea,* and other taxa, comprises nearly five manuscript pages. Because most references cited are lists or repetitions of relatively few uncritical but far-reaching decisions, only the more important are discussed in the following species accounts.

Valve morphology and other characters of the syntypes indicate that *Acanthochitona spiculosa* is related to the group containing the Caribbean *A. astrigera*, the eastern Pacific *A. hirudiniformis* (Sowerby, 1832), and the Hawaiian *A. viridis* (Pease, 1872). However, the syntypes are so worn that they cannot be related with certainty to any of those species. The valves are somewhat wider and the dorsal tuft spicules are shorter, more coarse, and less numerous than are those of both *A. astrigera* and another Caribbean species described hereafter. The valves and spicules of *A. spiculosa* seem to most resemble those of *A. hirudiniformis*; if they prove to be conspecific, the latter name will have priority. No other specimens of Caribbean, Brazilian, or East Pacific *Acanthochitona* resemble the syntypes of *A. spiculosa*. Until the syntypes can be related with certainty to specimens of known locality, *A. spiculosa* should be considered a *species inquirenda.*

***Acanthochitona astrigera* (Reeve, 1847)**

Figs. 30-41

Chiton astriger Reeve, 1847: pl. 18, sp. and fig. 109.
Acanthochiton astriger, Dall, 1889a: 174, 175.
(?) *Chiton (Acanthochiton) astriger,* E. A. Smith, 1890: 496, 497.
Acanthochites spiculosus var. *astriger,* Pilsbry, 1893: 22, 23, pl. 13, figs. 55-57.
Acanthochitona spiculosa, Kaas, 1972: 46-49 (pars) *non A. spiculosa* (Reeve, 1847).
Acanthochitona astriger, Watters, 1981: 173 (pars, *non* pl. 2d, pl. 4h).
Acanthochitona astrigera, Lyons, 1983: 91. Ferreira, 1985: 205-207 (pars).

TYPE MATERIAL: LECTOTYPE: 19.0 mm, Barbados, BM(NH) 19809/4 (herein designated). PARALECTOTYPES: 3 spec., 19.5-22.0 mm, collected with lectotype, BM(NH) 19809/1-3.

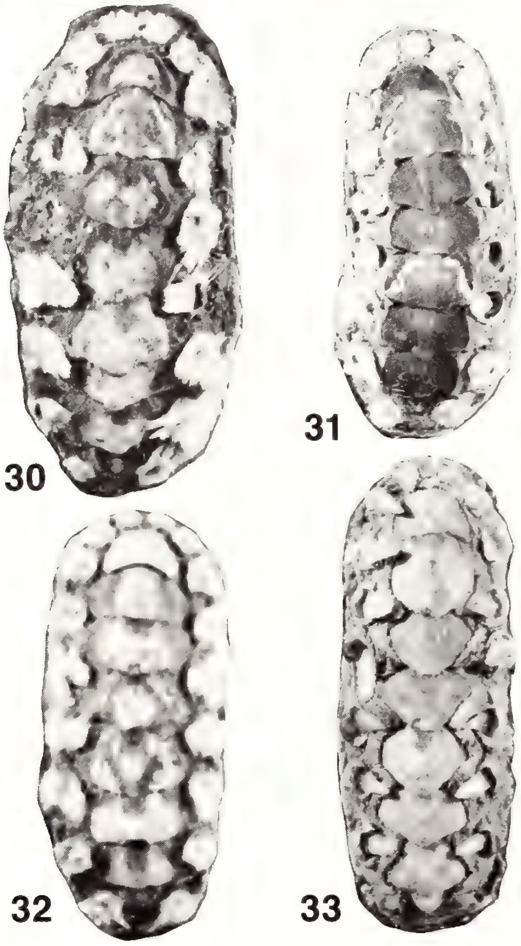
OTHER MATERIAL EXAMINED: BAHAMAS: 30 spec., 11.5-19.0 mm, Eight Mile Rock, Grand Bahama, intertidal, 21-23 May 1981, FSBC I 32527. —3 spec., 9.4-12.7 mm, Bartlett Hill, Eight Mile Rock, Grand Bahama, intertidal, 29 Aug 1984, FSBC I 32038. —28 spec., 9.9-21.5 mm, Hunters, Grand Bahama, intertidal, 29 Aug 1984, FSBC I 32037. —5 spec., Silver Cove Canal, Freeport, Grand Bahama, 0.5-1.5 m, 28 Aug 1984, FSBC I 32036. —1 spec., curled, Grand Bahama, RMNH K3730. —1 spec., Chub Cay, intertidal, M. Williams collection. DOMINICAN REPUBLIC: 3 valves, Playa Embassy, 16 km east of Boca Chica, beach drift, Bullock collection. CAYMAN ISLANDS: 2 spec., 14.0, 15.0 mm, Jackson's Point, Grand Cayman, 0-0.5 m, 9 June 1973, RMNH. ST. MAARTEN: 1 spec., 16.9 mm, W. Long Beach, RMNH K4952. BARBADOS: 1 spec., 23.5 mm, Archers Bay, St. Lucy, 5 Sept 1970, Bullock collection. BONAIRE: 7 spec., 11.7-25.2 mm, Kralendijk, intertidal, 9 Oct 1986, FSBC I 32528. CURAÇAO: 2 spec., 13.5, 18.7 mm, Port Marie, 16-18 Apr 1966, Bullock collection.

TYPE LOCALITY: Barbados (original designation).

DISTRIBUTION: Grand Bahama Island to Grand Cayman Island, Barbados, Bonaire, and Curaçao; intertidal or very shallow depths.

DESCRIPTION OF TYPES: All four types (Figs. 30-33) previously glued to tablet, later removed; 3 glued by ventral surface, 1 by dorsal surface. Foot and viscera remaining in all specimens.

Overall shape elongate, relatively slender, with dimensions 22 x 8 mm, 22 x 10 mm, 19.5 x 8 mm, 19 x 7.5 mm.



Figs. 30-33. *Acanthochitona astrigera* (Reeve, 1847), type specimens; Barbados. **Fig. 30.** Paralectotype, 22.0 mm; BM(NH) 19809/1. **Fig. 31.** Lectotype, 19.0 mm; BM(NH) 19809/4. **Figs. 32, 33.** Paralectotypes, 19.5, 22.0 mm; BM(NH) 19809/3, 2.

Three of four specimens encrusted to varying degrees by coralline algae, although some valves have been cleaned. Valves of smallest specimen in excellent condition.

Girdle brown, encroaching over anterolateral areas of valves so that intermediate valves are shield-shaped. Valve color varying from brown with white maculations laterally to dark blue-green, approaching black; where tegmentum damaged, underlying shell blue-green. Tegmentum covered with small pustules, drop-shaped near jugum, more ovate near center. Pustules of valve i small, ovate near apex, larger, drop-shaped near margins. Jugum of intermediate valves slender, with nearly smooth surface rendered finely striate by linear arrangement of fine pits near margins, pits exposed across entire jugal width near beaks; subsurface striations visible through smooth jugum surface in remaining areas. Valve viii with drop-shaped to ovate pustules as on other valves; mucro relatively low, posterior of center; jugum smooth, but with longitudinal striae visible beneath transparent surface.

Spicules of anterior and sutural girdle tufts extremely dense, white, straight, very slender; numerous very small spicules on dorsum of girdle; spicules at girdle margin stout, long, approximately ⅓ length of those in tufts, overlying shorter, sharp-tipped spicules, both types glassy, white; underside of girdle with very fine, short spicules protruding through. Fragments of foraminifera and carbonate particles trapped among girdle spicules.

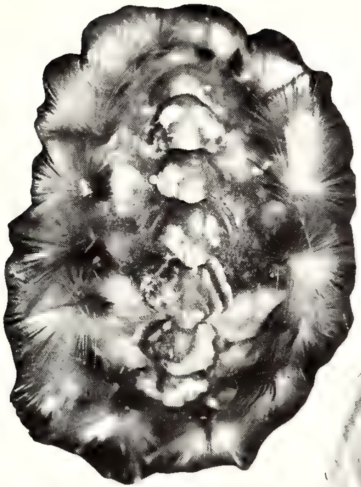
SUPPLEMENTAL DESCRIPTION: Largest specimen (FSBC I 32528) 25.2 mm long, 15.0 mm wide; valves occupying about 30% total specimen width (Fig. 34). Valves dark blue-green to black, usually with white, stripe-like maculations on valves ii and v, less commonly on other valves. Girdle blue-green, brown, or black, virtually obscured by expanded tufts of long, slender spicules.

Valve i semilunate (Fig. 35), wider than long, posterior margin straight, with anterior insertion plate bearing 5 slits; tegmentum occupying approximately 70% of valve length. Intermediate valves ii-vii beaked posteriorly, with smooth jugum widening anteriorly (Figs. 36, 37); tegmentum pentagonal, as long as wide in all but smallest specimens, with straight to slightly convex anterolateral margins; sutural laminae large, broad, curving anteromedially from posterolateral corners of tegmentum, with broadly to acutely rounded tips separated by broad sinus; single narrow slits along lateral margins. Valve viii tegmentum trigonal (Figs. 38-40), widest anteriorly, with anterior margin straight at broad sinus; mucro elevated, posterior of center; sutural laminae very well-developed, broad, slightly or markedly sinuous along margins; two slits in posterior insertion plate distinct, varying in width and depth. Valve viii often misshapen, asymmetrical or missing features (Figs. 39, 40). Pustules of tegmentum ovate to drop-shaped (Fig. 41), shallowly cupped, 80-90 µm long, constricted adapically, with single, large, macresthete, 1-3 micresthetes at juncture of apex and tegmental plain.

Girdle upper surface dominated by 18 anterior and sutural tufts each comprised of more than 100 white to light amber, long (to 4 mm), slightly curved, slender, sharp-tipped spicules; background spicules of dorsal surface short (100 µm), straight, sharp-tipped, blue, brown, or black; marginal spicules white, approximately 500 µm long, straight, slender, sharp-tipped; underside covered with fine (80 µm), sharp-tipped spicules directed toward periphery.

DISCUSSION: The dark blue-green valves, densely packed, long, slender, sharp-tipped spicules of anterior and sutural girdle tufts, and white maculations on the blue-green tegmentum, often only on valves ii and v, leave no doubt that specimens reported here as *Acanthochitona astrigera* are conspecific with those described by Reeve. Bullock's 23.5 mm specimen from Barbados is identical in all respects with Reeve's syntypes. Reeve's smallest specimen, illustrated in Fig. 31, is designated herein as lectotype.

E. A. Smith (1890) initiated the confusion between *Acanthochitona astrigera* and *A. spiculosa* with the statement: "[Reeve's] figure (47) of the detail of sculpture of *C. spiculosa*, Reeve, which I believe to be the same species [as *C. astrigera*], gives quite as good an idea of the ornamentation [of *astrigera*] as [Reeve's] figure 109." Pilsbry's (1893) diagnostic comments indicate that he correctly recognized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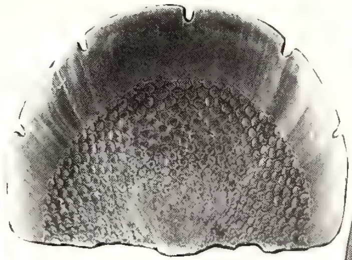
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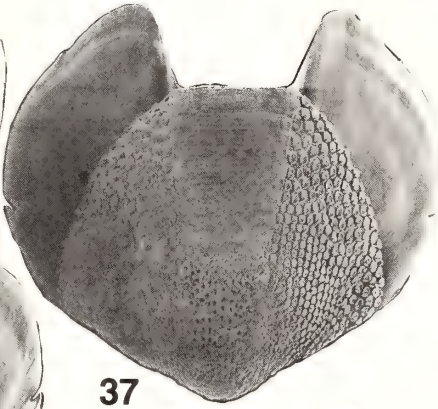
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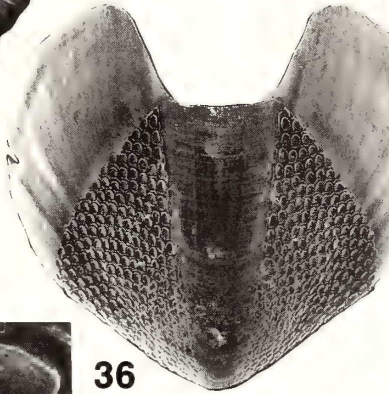
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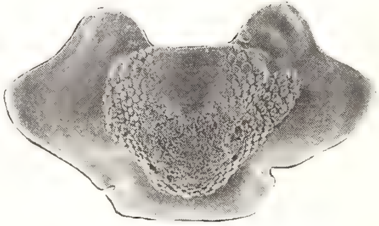
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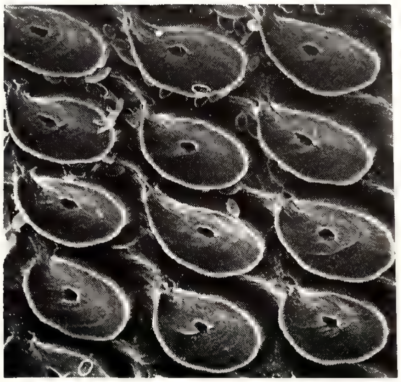
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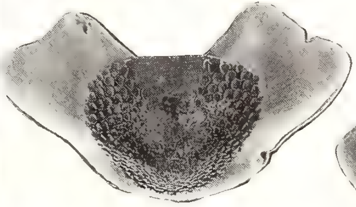
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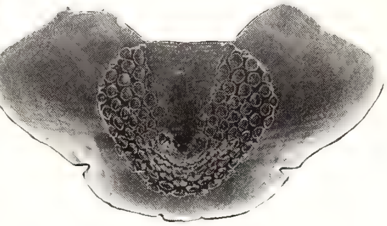
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Figs. 34-41. *Acanthochitona astrigera* (Reeve, 1847). **Fig. 34.** Whole specimen, 20.2 mm; Eight Mile Rock, Grand Bahama; FSBC I 32527. **Fig. 35.** Valve i *ex* 15.0 mm specimen; same lot. **Fig. 36.** Valve iv, same specimen. **Fig. 37.** Valve v *ex* 18.1 mm specimen; same lot. **Fig. 38.** Valve viii *ex* 12.2 mm specimen, same lot. **Fig. 39.** Valve viii, same specimen as 35. **Fig. 40.** Valve viii, same specimen as 37. **Fig. 41.** Tegmental pustules, valve iv, same specimen as 38 (field width = 280 μm).

A. astrigera, but he cited Smith as authority in designating *astrigera* a variety of *A. spiculosa* despite the fact that Smith chose to use *astrigera*, not *spiculosa*, for his material. Pilsbry cited no material of *A. spiculosa s.s.* Thereafter, *A. astrigera* was reported by many authors under the name *A. spiculosa*, as were many specimens of *A. pygmaea* and other taxa. Kaas (1972) reported as *A. spiculosa* specimens of *A. astrigera* from Grand Bahama Island, but he also reported some specimens of *A. pygmaea* as *A. spiculosa* (see remarks for that species). Watters (1981) correctly noted that *A. astrigera* and *A. spiculosa* were distinct, but he included an undescribed species within his concept of *A. astrigera*, and he supported Dall's misconception that *A. spiculosa* represented the species otherwise known as *A. pygmaea* (Pilsbry, 1893). Ferreira (1985) followed Watters' concepts of both *A. astrigera* and *A. spiculosa*.

Thus, published records of *Acanthochitona spiculosa* and *A. astrigera*, its supposed synonym, actually include *A. astrigera, A. pygmaea,* and, according to material I have examined, some specimens of *A. andersoni* Watters, 1981, and a new species described hereafter. Specimens illustrated as *A. astrigera* by Watters (1981) from La Parguera, Puerto Rico, and Water Id., Virgin Islands, are the new species. Likewise, Ferreira's (1985) record of *A. astrigera* from Belize was based upon an IRCZM specimen of the new species. The literature can be corrected only when previously reported specimens, including E. A. Smith's Fernando Noronha record, have been re-examined.

Dall (1889a) listed *Acanthochitona astrigera* from Dry Tortugas and the Florida Keys, but I have seen no specimens from Florida. At Grand Bahama Island, *A. astrigera* lives principally among brown algae in the intertidal zone of high wave energy, rocky shores, a habitat absent from the Florida Keys.

The relationship of *Acanthochitona astrigera* to other New World *Acanthochitona* is discussed under remarks for the new species.

Acanthochitona lineata* Lyons, *sp. nov.

Figs. 42-51

Acanthochitona astriger, Watters, 1981 (pars, pl. 2d, pl. 4h). *Acanthochitona astrigera,* Ferreira, 1985: 206-208 (pars, Belize). [*non A. astrigera* (Reeve, 1847)].

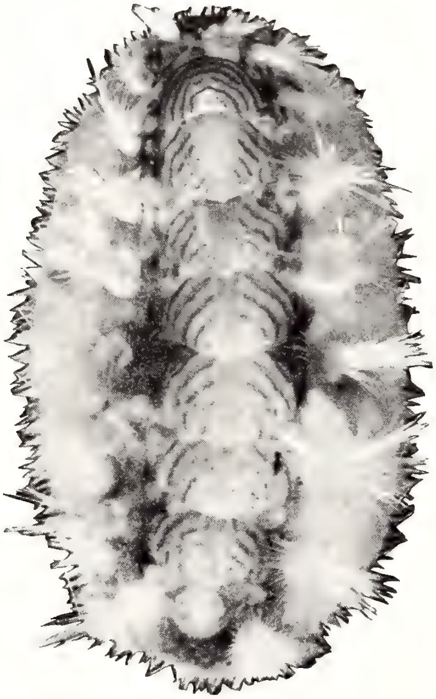
TYPE MATERIAL: HOLOTYPE: 19.5 mm x 10.5 mm, Silver Cove Canal, Freeport, Grand Bahama Island, 0.5-1.5 m, 28 Aug 1984, W. G. Lyons, collector, USNM 859315. PARATYPES: BAHAMAS: 1 spec., 10.8 mm, Bartlett Hill, Eight Mile Rock, Grand Bahama, 0-0.5 m, 29 Aug 1984, FSBC I 32434. —34 spec., 5.6-22.5 mm, same locality and date as holotype, ANSP A12122 (2), RMNH 55986 (2), FSBC I 32433 (29). —2 spec., 22.6, 33.0 mm, McLeanstown, east end Grand Bahama, 1 m, 27 Aug 1984, FSBC I 32432. PUERTO RICO: 4 spec., 7.0-11.1 mm, Magueyes Id., La Parguera, 1967, Bullock collection. —16 spec., 8.5-13.9 mm, Magueyes Id., Bullock collection (12), FSBC I 32565 (4). —1 spec., 21.4 mm, Media Luna Reef, La Parguera, 0-2 m, 15 Aug 1985, FSBC I 32435. —1 spec., 21.8 mm, Cayo Enrique, La Parguera, 0-1 m, 19 Aug 1985, FSBC I 32436. VIRGIN ISLANDS: 1 spec., 9.7 mm, Water Id., July 1959, DMNH 95381. BELIZE: 1 spec., 20.0 mm, Carrie Bow Cay, 0-1 m, 23 Mar 1981, IRCZM 61:052.

TYPE LOCALITY: Silver Cove Canal, Freeport, Grand Bahama Island.

DISTRIBUTION: Grand Bahama Island to Puerto Rico, the Virgin Islands, and Belize, 0.5-2.0 m.

DESCRIPTION: Largest specimen 33.0 mm long, 18.0 mm wide including girdle; valves occupying approximately 30% of total specimen width (Figs. 42-44). Valve i with 6-8 olivaceous, equally spaced concentric lines, expressed on valves ii-vii as 3-7 transverse stripes (chevrons) extending posterolaterally from jugum; stripes varying in strength and number among individual specimens, usually strongest, most numerous, on valves i-iii; valves iii-v occasionally dark green, brown, or black, obscuring stripes; valve viii mostly white, with single large spots on lateral areas. Girdle entirely white or buff, sometimes mottled with brown or blue-green bands, occasionally with large brown or black spot near middle.

Valve i semilunate (Fig. 45), wider than long, posterior margin straight, with anterior insertion plate bearing 5 slits; tegmentum occupying 80-90% of valve length. Valves ii-vii strongly produced posteriorly; tegmentum pentagonal, with straight to slightly convex anterolateral margins (Fig. 46); sutural laminae well-developed, curving anteromedially from posterior corners of tegmentum, with subacute anterior tips separated by relatively narrow sinus; single slits on lateral margins. Valve viii tegmentum ovate (Fig. 47), widest lateromesially; mucro elevated, slightly posterior of center; sutural laminae well-developed, broadly subquadrate; two slits in posterior insertion plate very large. Proportions of small specimens may differ from those of larger individuals (Figs. 48-50).



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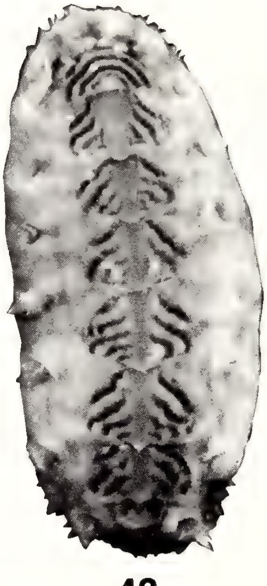

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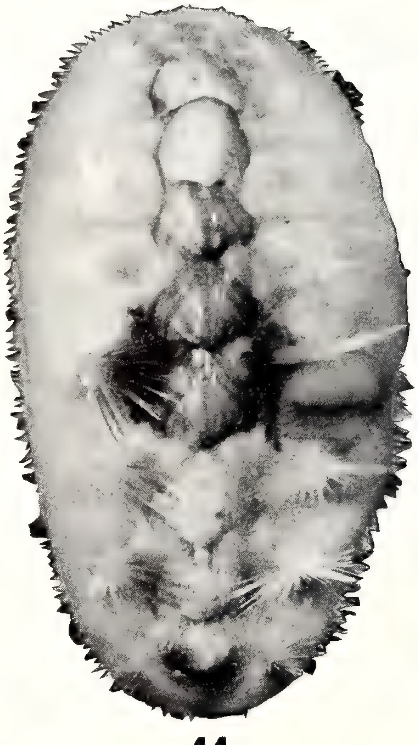

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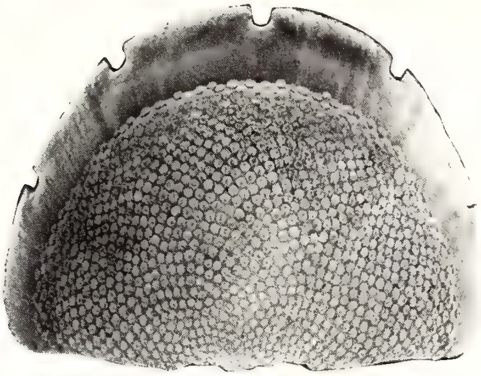
Figs. 42-44. *Acanthochitona lineata* Lyons, *sp. nov.* **Fig. 42.** Holotype, 19.5 mm; Freeport, Grand Bahama; USNM 859315. **Fig. 43.** Paratype, 13.1 mm; La Parguera, Puerto Rico; FSBC I 32565. **Fig. 44.** Paratype, 33.0 mm; McLeanstown, Grand Bahama; FSBC I 32432.



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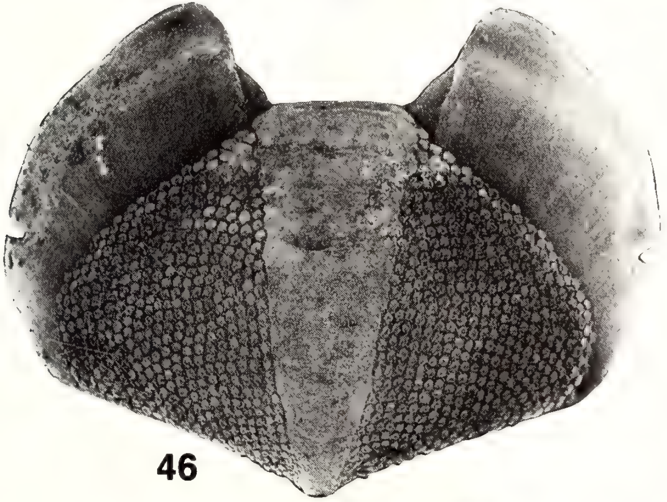

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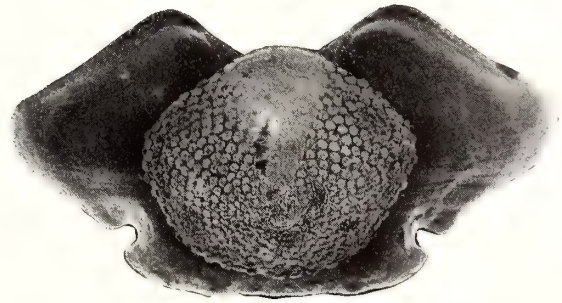

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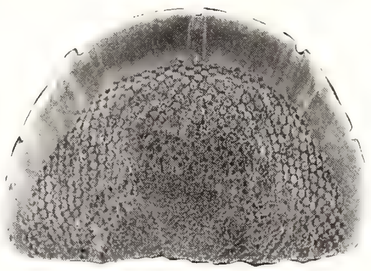

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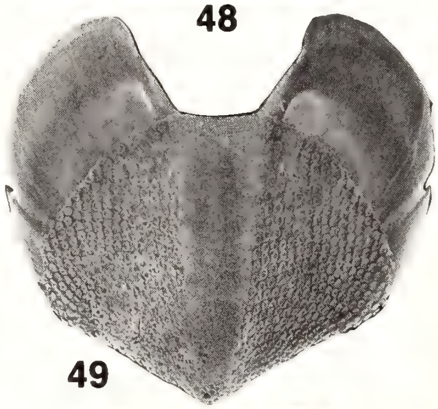

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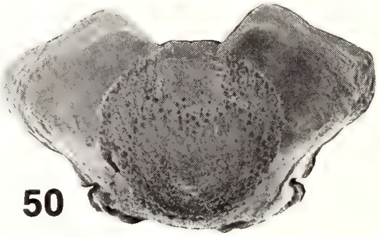

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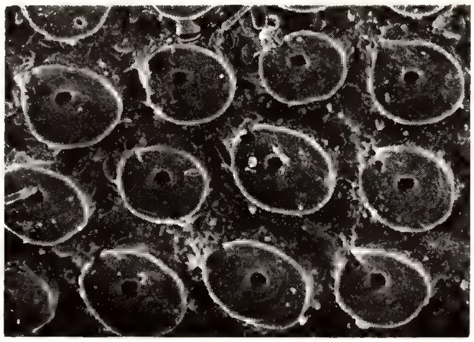

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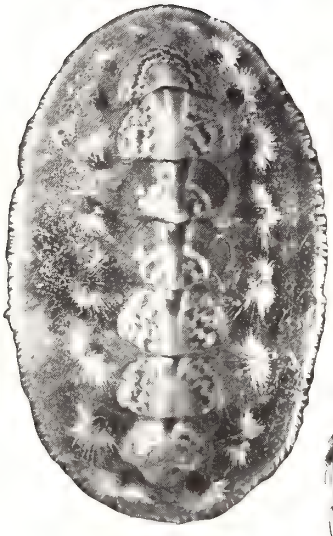
Figs. 45-51. *Acanthochitona lineata* Lyons, *sp. nov.* **Fig. 45.** Valve i *ex* 16.5 mm paratype; Freeport, Grand Bahama; FSBC I 32433. **Fig. 46.** Valve iv, same specimen. **Fig. 47.** Valve viii, same specimen. **Fig. 48.** Valve i *ex* 12.0 mm paratype; La Parguera, Puerto Rico; FSBC I 32565. **Fig. 49.** Valve iv, same specimen. **Fig. 50.** Valve viii, same specimen. **Fig. 51.** Tegmental pustules, valve iv, same specimen (field width = 280 μm).

Jugum smooth, relatively narrow on valves ii-vii, wide anteriorly on valve viii. Tegmentum of all valves covered evenly with small (50 μm), round to slightly ovate, shallowly cupped pustules (Fig. 51) with single, central macresthete, 1-2 micresthetes near apex.

Girdle upper surface appearing smooth, actually covered with extremely fine (20-30 μm) spicules; 18 anterior and sutural dorsal tufts comprised of more than 100 white, occasionally amber, long (to 3.5 mm), straight, very slender, sharp-tipped spicules; marginal spicules white, approximately 800 μm long, straight, slender, sharp-tipped; underside covered with fine (80 μm), sharp-tipped spicules directed toward periphery.

DISCUSSION: *Acanthochitona lineata* is related closely to *A. astrigera* of the Caribbean Sea and to *A. hirudiniformis* (Sowerby, 1832) (Figs. 52-56) of the tropical eastern Pacific Ocean; valves of all three species are quite similar. However, the tegmentum of valve viii of *A. astrigera* is widest anteriorly, whereas those of *A. lineata* and *A. hirudiniformis* are widest



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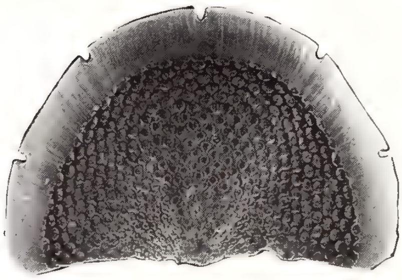

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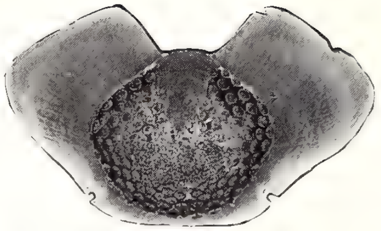

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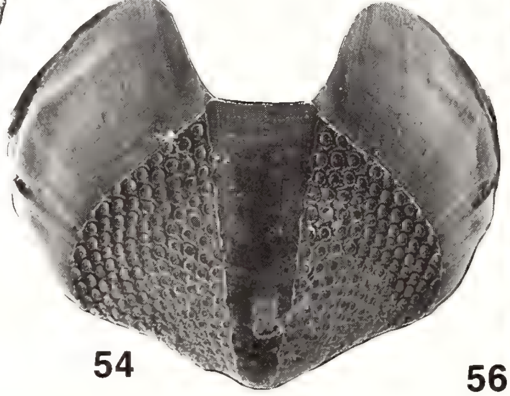

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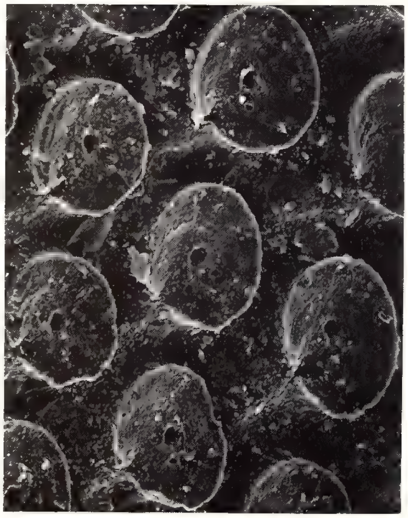

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Figs. 52-56. *Acanthochitona hirudiniformis* (Sowerby, 1832). **Fig. 52.** Whole specimen, 23.0 mm; Playa de Jaco, Costa Rica; FSBC I 32566. **Fig. 53.** Valve i *ex* 14.5 mm specimen, same lot. **Fig. 54.** Valve iv, same specimen. **Fig. 55.** Valve viii, same specimen. **Fig. 56.** Tegmental pustules, valve iv, same specimen (field width = 265 μm).

mesially. In addition, tegmental pustules of *A. astrigera* are drop-shaped, whereas pustules of the other two species are round, those of *A. hirudiniformis* being approximately 50% larger than those of *A. lineata* on specimens of similar size. Other differences which separate *A. hirudiniformis* from *A. lineata* include the longer spicules of the girdle mat, which give a rough rather than smooth appearance to the dorsal surface, the short green greater than long white spicules of the anterior and sutural tufts, and the diffuse rather than clearly demarked color pattern on the tegmentum. Like *A. astrigera, A. hirudiniformis* lives intertidally on high energy rocky shores, whereas *A. lineata* usually occupies shallow, subtidal, relatively more placid areas such as reef flats.

Ferreira (1985) identified the IRCZM specimen of *Acanthochitona lineata* from Carrie Bow Cay, Belize, as *A. astrigera*. The specimen from Water Id., Virgin Islands (DMNH 95381, not 45381) illustrated as *A. astrigera* by Watters (1981: 176, pl. 4h) also is *A. lineata*.

Specimens of *Acanthochitona lineata* I examined seldom exceeded 22 mm length. The 33 mm specimen (FSBC I 32432) was collected among many large (30-50 mm) *A. hemphilli* at the base of a colony of finger coral, *Porites astreoides*.

ETYMOLOGY: From Latin, *"linea"*, to denote the lines or stripes on the tegmentum.

Acanthochitona worsfoldi Lyons, *sp. nov.*

Figs. 57-65

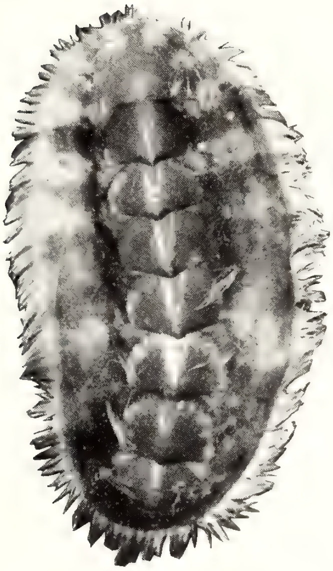
(?) *Choneplax* cf. *lata,* Ferreira, 1985: 208-213 (pars, figs. 16, 17). [*non Choneplax lata* (Guilding, 1829)].

TYPE MATERIAL: HOLOTYPE: Length 14.8 mm, width 6.7 mm, Silver Cove Canal, Freeport, Grand Bahama Island, 0.5-1.5 m, 28 Aug 1984, W. G. Lyons, collector, USNM 859318. PARATYPES: BAHAMAS: 6 spec., 7.7-17.2 mm, same locality and date as holotype, ANSP A12123 (1), FSBC I 32545 (5). —2 spec., 9.0, 13.6 mm, Tamarind Beach Reef, Grand Bahama, 18 m, 28 Aug 1984, RMNH 55987 (1), FSBC I 32544 (1). —2 spec., 7.0, 10.1 mm, Tamarind Beach Reef, 39 m, Sept 1983, FSBC I 32543. —1 spec., 13.5 mm, Gold Rock, Grand Bahama, 24.4 m, 1980, FSBC I 32541. —5 spec., 8.5-12.0 mm, Gold Rock, 24.4 m, Aug 1983, FSBC I 32542. —1 spec., 10.0 mm, 2 km off Bell Channel, Lucaya, Grand Bahama, 18.3-19.8 m, 6 Apr 1974, FSBC I 32539. —1 spec., 12.0 mm, 2 km off Bell Channel, Lucaya, 45.7 m, 10 July 1974, FSBC I 32540.

OTHER MATERIAL EXAMINED: 8 valves, Gold Rock, bottom sediments, 24.4 m, May-July 1981, FSBC I 32534. —53 valves, Grand Bahama, bottom sediments, May 1981, R. Quigley collection.

TYPE LOCALITY: Silver Cove Canal, Freeport, Grand Bahama Island.

DISTRIBUTION: Grand Bahama Island, 0.5-45.7 m, ? Barbados.



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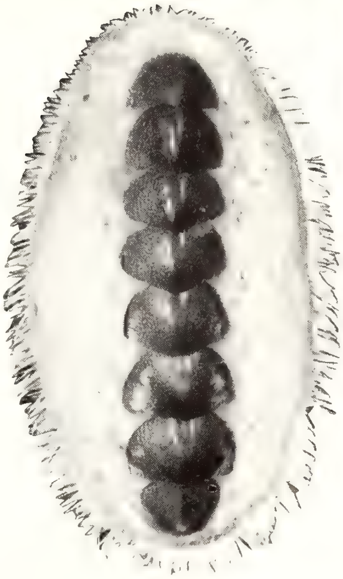

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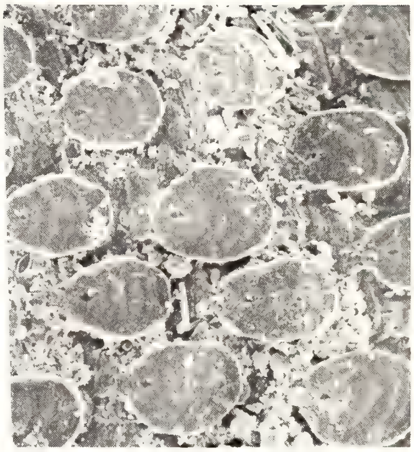

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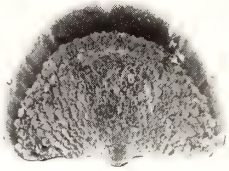

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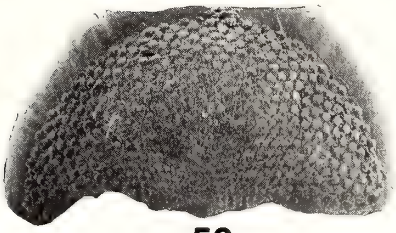

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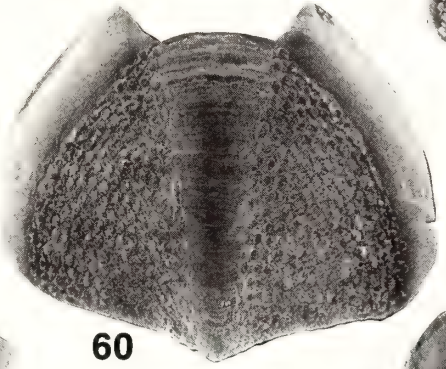

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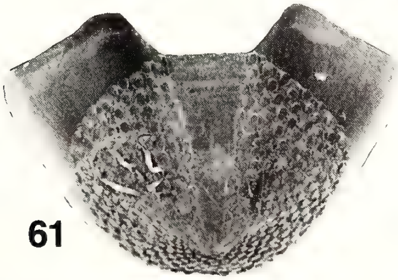

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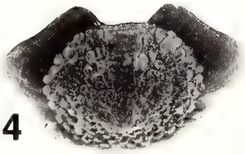

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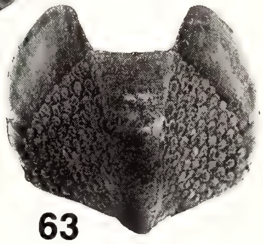

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Figs. 57-65. *Acanthochitona worsfoldi* Lyons, *sp. nov.* **Fig. 57.** Holotype, 14.8 mm; Freeport, Grand Bahama; USNM 859318. **Fig. 58.** Paratype, 17.2 mm; same location; FSBC I 32545. **Fig. 59.** Valve i *ex* 12.0 mm paratype; Gold Rock, Grand Bahama; FSBC I 32542. **Fig. 60.** Valve iv, same specimen. **Fig. 61.** Valve viii, same specimen. **Fig. 62.** Valve i *ex* 8.0 mm paratype; Freeport, Grand Bahama; FSBC I 32545. **Fig. 63.** Valve iv, same specimen. **Fig. 64.** Valve viii, same specimen. **Fig. 65.** Tegmental pustules, valve iv, same specimen (field width = 250 μm).

DESCRIPTION: Largest specimen 17.2 mm long, 7.4 mm wide including girdle; valves occupying about 40% of total specimen width (Figs. 57, 58). Valves highly arched, orange, rust, or bright red, with scattered white maculations on tegmentum. Girdle buff, usually crossed with reddish brown bars which continue onto spicular fringe at margin.

Valve i semilunate (Fig. 59), wider than long, posterior margin straight, with anterior insertion plate bearing 5 shallow slits; tegmentum occupying approximately 80% of valve length. Valves ii-vii beaked posteriorly (Fig. 60); tegmentum pentagonal to subcircular, rounded anteriorly, about as long as wide, with convex anterolateral margins; sutural laminae small, curving anteromedially from posterior corners of tegmentum; subacute anterior tips separated by wide, shallow sinus; single, small, narrow slits along lateral margins. Valve viii tegmentum subovate (Fig. 61), widest lateromesially, with straight anterior margin; mucro elevated, posterior of center; sutural laminae subrectangular, as wide or wider than long; two slits in posterior insertion plate small, V-shaped. Proportions of small specimens may differ from those of larger individuals (Figs. 62-64).

Jugum smooth, narrow at beaks, expanded anteriorly. Tegmentum of all valves covered evenly with small (50-60 μm), flattened subspatulate pustules (Fig. 65) with single subapical macresthete, 1-2 micresthetes at apex.

Girdle upper surface appearing smooth, actually covered with fine (50 μm) spicules; 18 anterior and sutural dorsal tufts comprised of 10-15 long (1.5 mm), slender, slightly curved, sharp-tipped, reddish brown or white spicules; margin densely fringed with long (1.0-1.2 mm), slender, slightly curved, sharp-tipped spicules similar to those in dorsal tufts; underside covered with fine (80 μm), narrow, straight, sharp-tipped spicules directed toward periphery.

DISCUSSION: *Acanthochitona worsfoldi* occurs in two color forms. The typical form, exemplified by the holotype (Fig. 57), has rusty orange valves, girdle, and spicules of the dorsal tufts and marginal fringe. Another form, represented by single specimens from 0.5-1.5 m and 38.0 m depths, has bright red valves, a light buff girdle, and only clear, vitreous spicules in the dorsal tufts and marginal fringe (Fig. 58). The two forms are identical morphologically.

Acanthochitona worsfoldi is distinguished from other species by its combination of large, subcircular tegmentum, small sutural laminae, few spicules in dorsal tufts, and dense marginal fringe of large spicules. Valve morphology suggests relationship to the species complex containing *A. astrigera* and *A. lineata*, but tegmental pustules and girdle spicules of those species differ considerably from those of *A. worsfoldi.*

The bathymetric range of *Acanthochitona worsfoldi* generally is greater than that of other Caribbean *Acanthochitona* species; eight of the nine lots examined were collected by divers using SCUBA. Ferreira (1985) diagnosed and illustrated specimens from Barbados which he tentatively assigned to *Choneplax lata.* I was unable to obtain that material for examination, but Ferreira's account suggests that the specimens are *A. worsfoldi*; if so, the range of *A. worsfoldi* would be extended considerably.

ETYMOLOGY: Named for Jack N. Worsfold, teacher and naturalist extraordinaire of Grand Bahama Island, whose collecting efforts contributed invaluably to many studies of marine invertebrates, including the present work.

***Acanthochitona pygmaea* (Pilsbry, 1893)**

Figs. 66-72

Acanthochiton spiculosus, Dall, 1889a: 174, 175 (pars). [*non A. spiculosa* (Reeve, 1847)].
Acanthochites pygmaeus Pilsbry, 1893: 23, pl. 13, figs. 58, 59.
Acanthochiton pygmaeus, Leloup, 1941: 37, figs. 2, 3, pl. 1, fig. 1 (? pars).
Acanthochiton spiculosa, Kaas, 1972: 46-49, figs. 74-81 (pars). Watters, 1981: 173-176, pl. 2a-c, pl. 4f, g. Ferreira, 1985: 214 (pars).
Acanthochitona pygmaea, Kaas, 1972: 49, 50, figs. 82-89 (? pars).

TYPE MATERIAL: PARALECTOTYPE: approximately 8.0 mm, partially disarticulated; Cedar Keys, Florida; ANSP 35782.

OTHER MATERIAL EXAMINED: FLORIDA: 27 spec., 6.4-14.1 m, St. Andrews Bay, Panama City, 1.3-2.0 m, Jan 1982, R. Granada collection (23), FSBC I 32474(4). —2 valves, Florida Middle Ground, 28°35'N, 84°18'W; bottom sediments, 25.6-38.1 m, 7 Mar 1976, FSBC I 32524. —9 spec., 6.4-13.1 mm, Cedar Keys, CAS 063316. —1 spec., off Crystal River, 1.8 m, 25 Mar 1968, FSBC I 6524. —2 spec., 11.0, 11.9 mm, Anclote Key, 11 Feb 1982, FSBC I 32063. —2 spec., 4.5, 7.4 mm, 6 km west of Anclote Key, 29 Sept 1982, FSBC I 32476. —28 spec., 2.0-9.0 mm, south end Anclote Key, 3-4 m, 1 Feb 1982, FSBC I 32475. —7 spec., 2.0-9.0 mm, south end Anclote Key, 3.5 m, 22 Sept 1982, FSBC I 32473. —5 spec., all curled, Gulfport, RMNH K3731. —6 spec., 12.9-15.5 mm, Tampa Bay, 0.5 m, 9 July 1978, FSBC I 32052. —16 spec., 4.5-16.6 mm, Sarasota Bay, 4 m, CAS 063318. —1 spec., curled, Charlotte Harbor, 2 m, FSBC I 8457. —9 spec., 5.0-11.1 mm, Punta Rassa, 4 m, CAS 063320. —32 lots, 544 spec., Hourglass Stations B, C, J, K (18-37 m) off St. Petersburg and Sanibel Id., eastern Gulf of Mexico, 1965-67. —8 spec., 4.0-9.8 mm, Key West, CAS 063321. —1 spec., 18.0 mm, No Name Key, CAS 063319. —3 spec., 6.0-12.0 mm, West Summerland Key, 0-1 m, 27 Sept 1981, FSBC I 32062. —3 spec., 9.1-13.0 mm, West Summerland Key, 1976, Bullock collection. —13 spec., 5.2-15.0 mm, West Summerland Key, 1978, Bullock collection. —1 spec., 10.0 mm, Sister Creek, Vaca Key, 0-1 m, 4 Oct 1979, FSBC I 32058. —7 spec., 4.5-9.4 mm, Sister Creek, 0.5-1.5 m, 5 Aug 1980, FSBC I 32060. —5 spec., 8.7-14.0 mm, north side Vaca Key, 0-1 m, 30 Sept 1979, FSBC I 32053. —4 spec., 10.7-13.8 mm, 1 spec., disarticulated, Bonefish Key, RMNH K2852. — 5 spec., 10.0-12.0 mm, Bonefish Key, CAS 063322. —1 spec., curled, Burnt Point, Crawl Key, 2.5 m, July 1982, FSBC I 32471. —1 spec., curled, Burnt Point, 4 Aug 1982, FSBC I 32472. —1 spec., 10.2 mm, northeast end Grassy Key, 0.5 m, 1 Oct 1979, FSBC I 32054. —1 spec., 11. 6 mm, north side Grassy Key, 0-1 m, 1 Oct 1979, FSBC I 32055. —12 spec., 6.2-10.7 mm, north side Grassy Key, 0.5-1.0 m, 5 Aug 1980, FSBC I 32061. —54 spec., 6.5-17.0 mm, Grassy Key Quarry, 0-2 m, Feb 1975-Aug 1980, 4 lots: FSBC I 32051, 32056, 32057, 32059. —19 spec., 6.2-17.2 mm, Duck Key, 23 Aug 1978, Bullock collection. —1 spec., 12.6 mm, Lower Matecumbe Key, CAS 063317. —1 spec., curled, off Hutchinson Id., 11.2 m, 17 Sept 1973, FSBC I 32523. —1 spec., 11.5 mm, Bethel Shoal, 9-15 m, 27 June 1978, IRCZM 61:014. BERMUDA: 2 spec., 12.4, 15.2 mm, Baileys Bay, July 1969, FSBC I 32522. BAHAMAS: 2 spec., 11.5, 12.0 mm, Deadmans Reef, Grand Bahama, 0.5-1.5 m, 25 May 1981, FSBC I 32469. —3 spec., 4.2-6.5 mm, West Hawksbill Creek, Grand Bahama, 28 June 1981, FSBC I 32470. —12 spec., 6.7-10.7 mm, Tamarind Beach Reef, Grand Bahama, 18 m, 28 Aug 1984, FSBC I 32064. —2 valves, Gold Rock, Grand Bahama, bottom sediments, 24.4 m, May-July 1981, FSBC I 32525. —9 valves, Grand Bahama, bottom sediments, May 1981, R. Quigley collection. —1 spec., 9.5 mm, McLeanstown, east end Grand Bahama, 1-2 m, 24 May 1981, FSBC I 32468. —1 spec., 14.0 mm, Green Turtle Cay, Abaco, 0.5 m, 3-9 May 1978, FSBC I 32466. —1 spec., 4.5 mm, Turtle Rocks near Bimini, 5.5 m, ANSP 325864. TURKS AND CAICOS ISLANDS: 1 spec., 21.0 mm, Providenciales, M. Williams collection. PUERTO RICO: 22 spec., 6.0-17.0 mm, Cayo Enrique, La Parguera, Apr 1966, Bullock collection. —8 spec., 8.5-17.7 mm, Cayo Enrique, 0.5-1.0 m, 15 Aug 1985, FSBC I 32066. —6 spec., 4.7-16.1 mm, Cayo Enrique, 0-1 m, 19 Aug 1985, FSBC I 32069. —1 spec., 10.0 mm, Cayo Enrique, May 1985, FSBC I 32071. —2 spec., 15.2, 17.9 mm, 3 km east of La Parguera, 1 m, 17 Aug 1985, FSBC I 32067. —1 spec., 11.8 mm, Media Luna Reef, La Parguera, May 1985, FSBC I 32070. —51 spec., 8.2-21.2 mm, Media Luna Reef, 0-2 m, 15-19 Aug 1985, FSBC I 32065. —3 spec., 8.4-20.2 mm, Isla Turramote, La Parguera, 0-2 m, 19 Aug 1985, FSBC I 32068. VIRGIN ISLANDS: 1 spec., disarticulated, St. Thomas, RMNH K4686. SABA BANK : 2 spec., 7.5, 9.0 mm, 17°12'N, 63°38'W, 26 m, 8 June 1972, RMNH. MEXICO: 2 spec., 5.0, 6.0 mm, 7 valves, Yucum Balam, 15 km north of Ciudad Campeche, TUDG collection. —4 valves, beach 19 km southwest of Champton, Campeche, TUDG collection. —4 valves, Isla Arenas, 80 km north of Ciudad Campeche, TUDG collection. —2 valves, Punta Palmar Lighthouse, Yucatan, TUDG collection. —7 valves, Isla Cerritos, 5 km west of San Felipe, Yucatan, TUDG collection. —1 spec., 13.0 mm, Isla Mujeres, Quintana Roo, 0-1 m, 29 Sept 1985, FSBC I 32072.

TYPE LOCALITY: Key West, Florida (by subsequent designation, Watters, 1981).

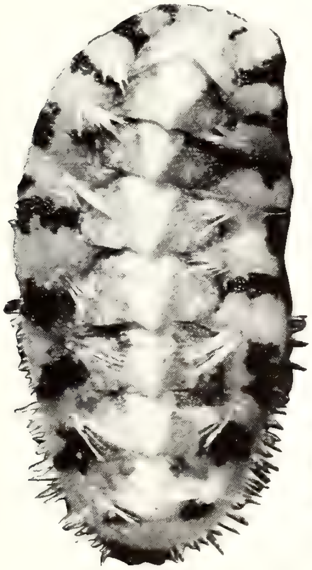
DISTRIBUTION: Bermuda, both coasts of Florida, Campeche to Quintana Roo, Mexico; Bahama Islands to Puerto Rico, Virgin Islands, and Saba Bank; intertidal to about 40 m.

DESCRIPTION: Largest specimen 21.2 mm long, 12.0 mm wide including girdle; valves occupying 40-45% total specimen width (Fig. 66). Valves green, orange, often white variegated with green or brown. Girdle buff or tan, usually with green, blue-green or black bars, sometimes with orange spots; dorsal spicular tufts green, blue-green or white; spicules of marginal fringe white, usually in combination with blue or magenta.

Valve i semilunate (Fig. 67), wider than long, broadly V-shaped or concave posteriorly, with anterior insertion plate bearing 5 slits; tegmentum occupying about 90% of valve length. Valves ii-vii beaked posteriorly (Figs. 68, 69); tegmentum ovate, about 1.6 times as wide as long, with convex anterolateral margins; sutural laminae with rounded to subacute anterior tips separated by broad sinus; single slits along lateral margins. Valve viii trigonal (Fig. 70), widest at anterolateral tips, rounded posteriorly; tegmentum ovate, slightly wider than long; mucro prominent, subcentral; sutural laminae flared anterolaterally, with straight or concave anterior margins; 2 narrow slits in posterior insertion plate.

Jugum expanded anteriorly, with distinct longitudinal incisions usually over entire length, sometimes rubbed smooth anteriorly, lateral margins irregularly merging with pustules of tegmentum. Tegmental pustules shallowly cupped, ovate to drop-shaped (Fig. 71), about 120 μm long, 70 μm wide, with central macresthete, 3-6 micresthetes.

Girdle upper surface covered densely with slender, vitreous, sharp-tipped spicules about 100-150 μm long; 18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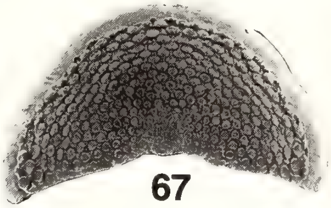
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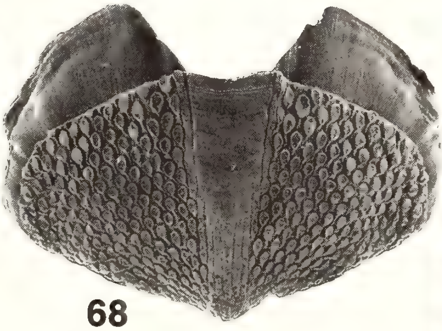
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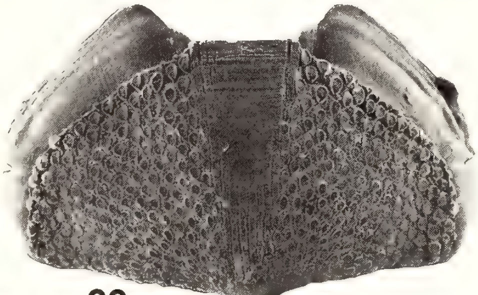
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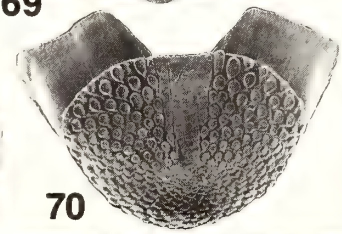
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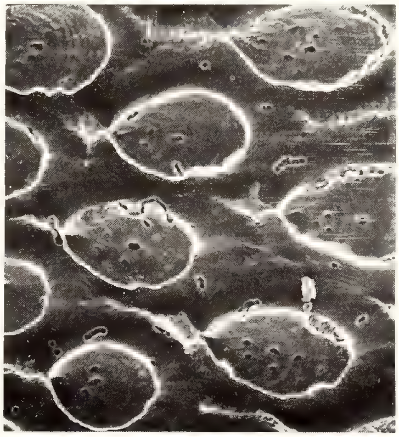
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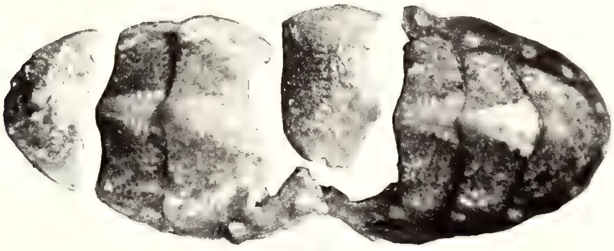
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Figs. 66-72. *Acanthochitona pygmaea* (Pilsbry, 1893). **Fig. 66.** Whole specimen, 12.2 mm; Grassy Key, Monroe County, Florida; FSBC I 32056. **Fig. 67.** Valve i *ex* 13.2 mm specimen; Tampa Bay, Florida; FSBC I 32052. **Fig. 68.** Valve iv, same specimen. **Fig. 69.** Valve v, same specimen. **Fig. 70.** Valve viii, same specimen. **Fig. 71.** Tegmental pustules, valve iv, same specimen (field width = 235 μm). **Fig. 72.** Paralectotype, 8.0 mm; Cedar Keys, Florida; ANSP 35782.

anterior and sutural tufts comprised of 100 or more very slender, straight, sharp-tipped spicules to 2.2 mm long; margin fringed with straight, slender, vitreous, sharp-tipped spicules to 700 μm long; underside covered with short (80 μm), sharp, vitreous spicules directed toward periphery.

DISCUSSION: Pilsbry (1893) described *Acanthochitona pygmaea* based upon specimens from Cedar Keys and Key West, Florida; his illustrations (pl. 13, figs. 58, 59) were of a single intermediate valve with strongly incised jugum and an enlarged view of tegmental pustules. Watters (1981) published a photograph of an intact 9 mm specimen from Key West and designated it the lectotype (ANSP 35783), although the partially disarticulated specimen from Cedar Keys (ANSP 35782) probably is the one Pilsbry illustrated. Watters' illustration of very wide valves and his description of a striated jugum indicate that the Key West lectotype and the Cedar Keys specimen are conspecific.

The Cedar Keys specimen (Fig. 72), now a paralectotype, is broken into five pieces: valves i-iii, valves vi-vii, valve viii, a broken intermediate valve (iv or v), and a fragment of that valve imbedded in a piece of the girdle. Overall length of the total specimen, estimated from its parts, is about 8 mm. The strongly incised jugum demonstrates that the specimen is conspecific with those reported as *Acanthochitona pygmaea* herein.

Despite a great quantity of literature which states otherwise, *Acanthochitona pygmaea* (Pilsbry, 1893) is not *A. spiculosa* (Reeve, 1847). That conclusion is supported by several observations: 1) there are no incisions on the jugum of *A. spiculosa*; 2) intermediate valves of *A. pygmaea* are much wider than long, whereas those of *A. spiculosa* are relatively more narrow; 3) the syntypes of *A. spiculosa* are considerably larger than nearly all of the 924 intact *A. pygmaea* examined herein; only two specimens of *A. pygmaea* were as large (21.0 mm, Turks and Caicos Ids., 21.2 mm, Puerto Rico) as the smallest of the five syntypes (21.0-33.0 mm) of *A. spiculosa*.

Because this species is so common in Florida and the northern Caribbean, most literature records of *Acanthochitona spiculosa* actually represent *A. pygmaea*. Dall (1889a) launched more than 90 years of taxonomic turmoil by including Cedar Keys, west Florida, and the Florida Keys within the range of *A. spiculosa*, indicating that his concept of *A. spiculosa* included the species Pilsbry later described as *A. pygmaea*. *A. pygmaea* is the only species of *Acanthochitona* which occurs at Cedar Keys and nearshore west Florida. Likewise, the *A. spiculosa* of Bermuda (Peile, 1926; Jensen and Harasewych, 1986) is *A. pygmaea*. Among material I examined were specimens of *A. pygmaea* previously identified as *A. spiculosa* by Kaas (RMNH), Watters (Bullock collection), and Ferreira (CAS, IRCZM). Leloup (1941) recognized *A. pygmaea* and illustrated valve viii of a specimen from Florida, but specimens he reported from Venezuela and Colombia could have been a new species described hereafter. Kaas (1972) treated *A. pygmaea* and *A. spiculosa* separately, but specimens he reported as *A. spiculosa* from Gulfport (RMNH K3731) and Bonefish Key (RMNH K2852), Florida, are *A. pygmaea*. It is doubtful that the specimens Kaas reported as *A. pygmaea* were that species, as evidenced by his description of only 12-15 spicules in dorsal tufts and other features more characteristic of several other species.

Where both species occur together in Florida and the northern Caribbean, it is not uncommon to find specimens of *Acanthochitona andersoni* in lots of *A. pygmaea*. Lots examined here that included both species are CAS 063321, collected at Key West by Hemphill; ANSP 325864, a paratype lot of *A. andersoni* Watters; and two unnumbered lots from West Summerland Key in the Bullock collection.

Acanthochitona pygmaea is common in Florida, the Bahama Islands, Yucatan, and Puerto Rico, but I have seen no specimens southward from Saba Bank. In addition to Leloup's (1941) records from Venezuela and Colombia, *A. pygmaea* has been reported from several locations in Brazil by Righi (1971), who illustrated only the short dorsal spicules, marginal spicules, and radula; those records need confirmation.

Acanthochitona venezuelana* Lyons, *sp. nov.
Figs. 73-80

TYPE MATERIAL: HOLOTYPE: Length approximately 20.0 mm (curled), North of La Guardia, Isla de Margarita, Venezuela, 12 June 1987, C. Franz, collector, USNM 859317. PARATYPES: 4 spec., all curled, approximately 16.0-19.0 mm, collected with holotype, FSBC I 32569 (2), RMNH 55988 (1), Bullock collection (1).

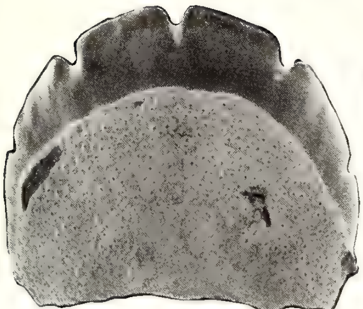
TYPE LOCALITY: North of La Guardia, Isla de Margarita, Venezuela.

DISTRIBUTION: Isla de Margarita, Venezuela.

DESCRIPTION: Largest specimen (holotype) approximately 20.0 mm long, 10.0 mm wide including girdle; valves occupying about 50% of total specimen width. Valves i-vii white with scattered black maculations arranged in vaguely concentric arcs anterior of beaks; jugum yellow-brown or mauve, usually with faint flush of mauve on tegmentum near beak. Valve viii with black maculation covering most of tegmentum. Girdle noticeably spiculose, tan to gray, with pale green spicules in anterior and sutural dorsal tufts.

Valve i semilunate (Fig. 73), wider than long, posterior margin straight, with anterior insertion plate bearing 5 U-shaped slits; tegmentum occupying approximately 70% of valve width. Valves ii-vii beaked posteriorly (Figs. 74, 75); tegmentum oblate, about 1.6 times as wide as long, with convex anterolateral margins; sutural laminae prominent, very wide, broadly rounded anteriorly, separated by wide, U-shaped sinus, with single deep slits along anterolateral margins. Valve viii pentagonal (Fig. 76), widest anterolaterally, dropping away rapidly behind posterior, elevated, prominently pointed mucro (Fig. 77); sutural laminae well-developed, markedly concave anteriorly, sharply produced at anterolateral corners; 2 narrow slits in posterior insertion plate.

Surface of jugum with smooth veneer overlying layer of numerous thin, longitudinal striae; both layers fragile, easily damaged, revealing honeycombed subjugal constructional elements beneath. Tegmentum of all valves with flat, oval pustules 220 μm long, elongate near jugum, smaller (130 μm),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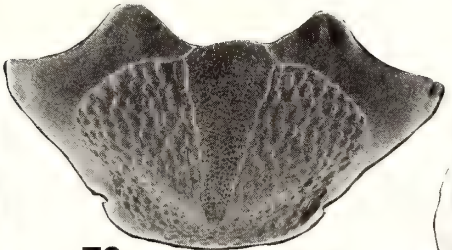
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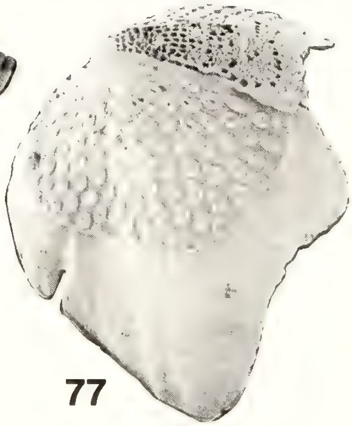
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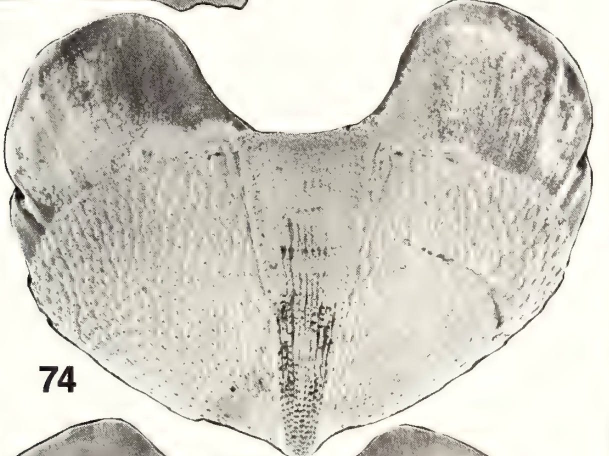
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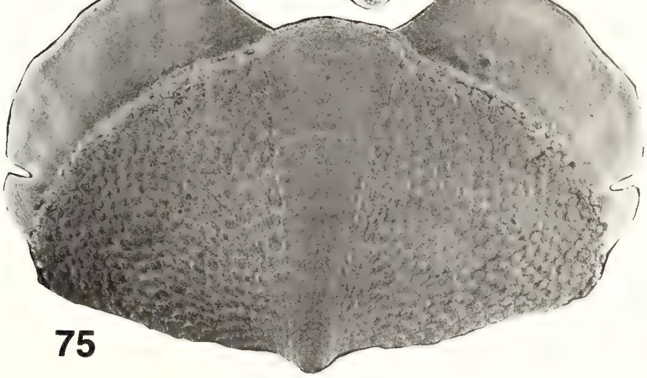
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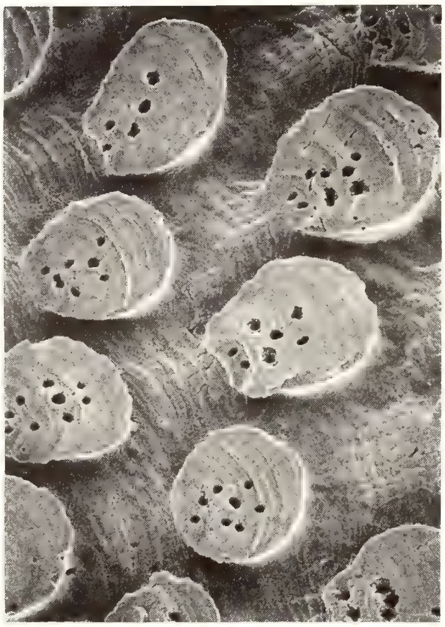
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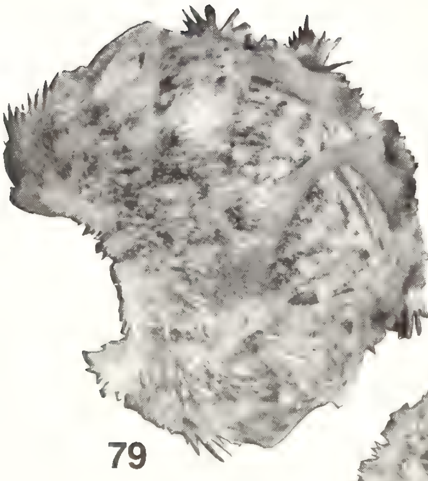
Figs. 73-78. *Acanthochitona venezuelana* Lyons, *sp. nov.* **Fig. 73.** Valve i *ex* 19.0 mm paratype; Margarita Id., Venezuela; FSBC I 32569. **Fig. 74.** Valve iv, same specimen. **Fig. 75.** Valve v, same specimen. **Fig. 76.** Valve viii, same specimen. **Fig. 77.** Valve viii, 18.0 mm paratype; same lot; lateral view. **Fig. 78.** Tegmental pustules, valve iv, same specimen (field width = 315 μm).

more rounded, subspatulate near outer margins (Fig. 78); macresthete subcentral, 5-8 micresthetes of nearly same diameter as macresthete clustered mostly on adapical half of pustule surface.

Girdle upper surface obviously spiculose, densely covered with straight to slightly curved, sharp-tipped, clear, glassy spicules (Figs. 79, 80), round in cross-section, about 300-600 μm long, overlying and generally obscuring mat of tiny (75 μm) slender spicules. Dorsal spicules gradually increasing in length to merge with marginal fringe, where they are longest (about 1 mm); no demarcation or change in form between dorsal and marginal spicules; 18 anterior and dorsal tufts with about 25 pale green, slender, straight, sharp-pointed spicules up to 1.5 mm long; lower surface covered with small (100 μm), densely packed, straight, slender spicules directed toward periphery.

DISCUSSION: *Acanthochitona venezuelana* most resembles *A. avicula* (Carpenter, 1864). Watters (1981) noted the relationship between the western Atlantic *A. pygmaea* (as *A. spiculosa*) and the eastern Pacific *A. avicula.* Like *A. pygmaea, A. avicula* has broad intermediate valves (Fig. 81), longitudinal incisions on the jugum, and drop-shaped pustules. *A. venezuelana* has broad valves with drop-shaped to spatulate pustules but lacks jugal incisions. Most notably, dorsal girdle spicules of *A. avicula* and *A. venezuelana* virtually are identical. The combination of high, pointed mucro, more narrow anterior end of the jugum, and possession of mostly ovate to subspatulate tegmental pustules separate *A. venezuelana* from *A. avicula.*



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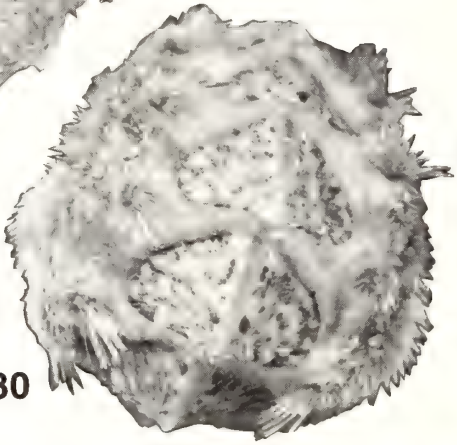

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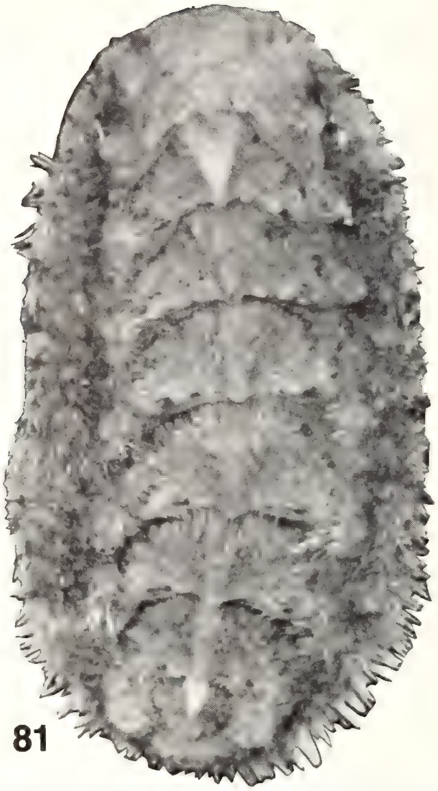

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Figs. 79, 80. *Acanthochitona venezuelana* Lyons, *sp. nov.* **Fig. 79.** Holotype, approximately 20.0 mm (curled), lateral view; Margarita Id., Venezuela; USNM 859317. **Fig. 80.** Holotype, dorsal view. **Fig. 81.** *Acanthochitona avicula* (Carpenter, 1864); entire specimen, 12.4 mm; Puertocitos, Baja California, Mexico; FSBC I 32570.

Acanthochitona avicula, *A. pygmaea* and *A. venezuelana* join *A. asterigera*, *A. hirudiniformis*, and *A. lineata* and *A. hemphilli*, *A. rhodea*, and *A. ferreirai* as groups with one eastern Pacific and two western Atlantic species. Although specimens of *A. venezuelana* have been seen only from Margarita Island, the species probably has a wider distribution across the Caribbean coast of South America and could replace *A. pygmaea* in that region. Dautzenberg (1900) reported a curled specimen (2.5 x 2.5 mm) of *A. pygmaea* dredged from 11 m at Los Testigos very near Isla Margarita, and Leloup (1941) reported a curled specimen (3 x 2.5 mm) of *A. pygmaea* dredged from 12-15 fm (22-27 m) off Cabo la Vela, Colombia; a specimen from Florida, not the southern Caribbean, was illustrated by Leloup (his fig. 2, reproduced as figs. 82-84 by Kaas, 1972). Kaas (1972) reported no specimens of *A. pygmaea* from farther south than St. Barts, Saba, and St. Eustatius, and I have seen no *A. pygmaea* from any area south of Saba Bank. Thus, it is possible that specimens reported by Dautzenberg and by Leloup as *A. pygmaea* could have been *A. venezuelana*.

ETYMOLOGY: Named for Venezuela, the Caribbean nation where the specimens were collected.

Acanthochitona roseojugum **Lyons, *sp. nov.***

Figs. 82-92

Acanthochitona pygmaea, Lyons, 1981: 36 (pars, Dry Tortugas sta. 2 only) [*non A. pygmaea* (Pilsbry, 1893)].

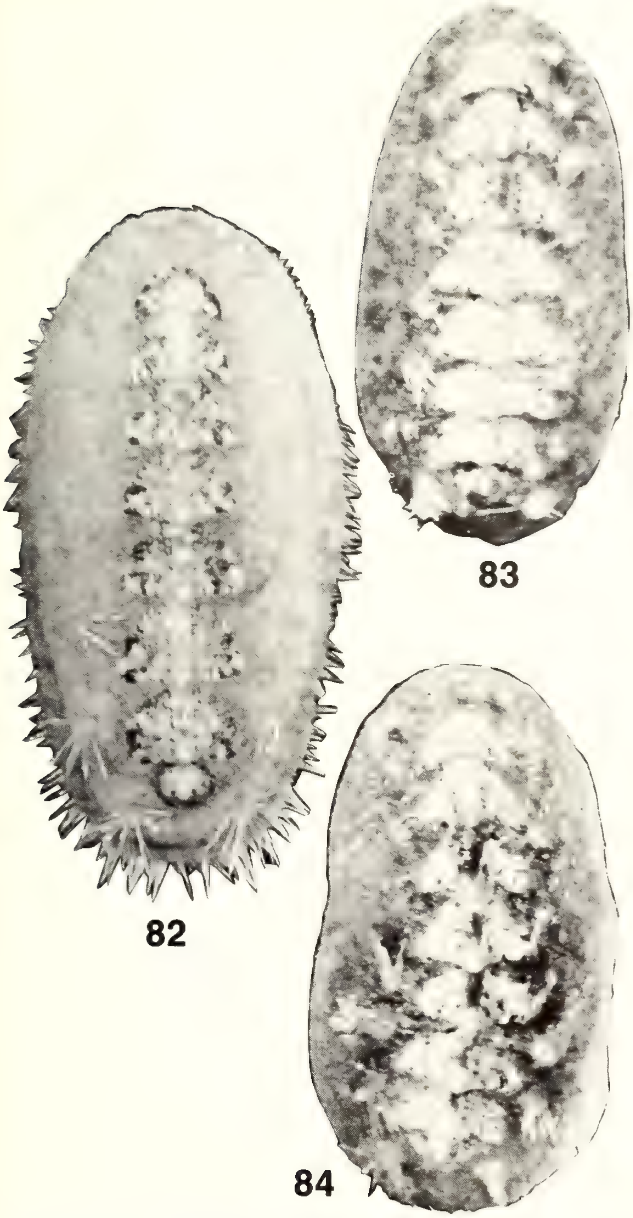
TYPE MATERIAL: HOLOTYPE: Length 12.2 mm, width 6.0 mm, Bartlett Hill, Eight Mile Rock, Grand Bahama Island, 0-0.5 m, 29 Aug 1984, W. G. Lyons, collector, USNM 859316. PARATYPES: FLORIDA: 4 spec., 8.1-8.7 mm, Bird Key Reef, Dry Tortugas, 0.5-1.0 m, 4 Oct 1979, FSBC I 32535. —1 spec., 6.4 mm, Florida Middle Ground, 28°35.0'N, 84°14.9'W, 31 m, 19 May 1977, FSBC I 24598. —1 spec., 10.6 mm, Peanut Id., Palm Beach Inlet, 0-1 m, 29 Aug 1982, FSBC I 32536. BAHAMAS: 4 spec., 10.0-12.2 mm (2 curled), collected with holotype, ANSP A12124 (1), RMNH 55989 (1), FSBC I 32537 (2). —1 spec., 12.4 mm, Caravel Beach, Freeport, Grand Bahama, 1 m, 30 Aug 1984, FSBC I 32538.

OTHER MATERIAL EXAMINED: FLORIDA: 1 valve, Florida Middle Ground, 28°38.1'N, 84°16.3'W, bottom sediments, 28.6 m, 21 May 1977, FSBC I 32533. —8 valves, Florida Middle Ground, 28°35'N, 84°18'W, bottom sediments, 25.6-38.1 m, 7 Mar 1976, FSBC I 32532. BAHAMAS: 4 valves, Gibson Cay, Andros, beach drift, 2 Sept 1971, FSBC I 32531. HONDURAS: 1 spec., 16.2 mm, Utila Id., June 1987, Sunderland collection.

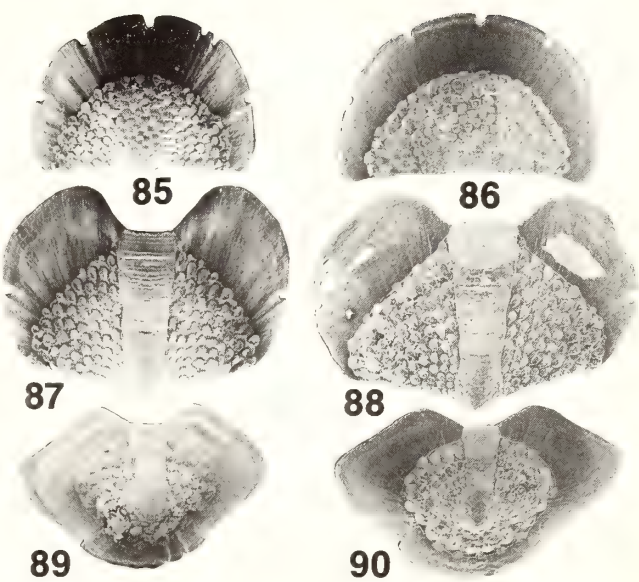
TYPE LOCALITY: Bartlett Hill, Eight Mile Rock, Grand Bahama Island.

DISTRIBUTION: Eastern Gulf of Mexico at Florida Middle Ground to Dry Tortugas, southeast Florida, the Bahama Islands, and Honduras; intertidal to 31 m.

DESCRIPTION: Largest specimen 16.2 mm long, 8.3 mm wide including girdle; valves occupying 30-35% of total specimen width (Figs. 82-84); tegmentum variously white with brown flecks or pale pinkish white variegated with greenish black;



Figs. 82-84. *Acanthochitona roseojugum* Lyons, *sp. nov.* **Fig. 82.** Holotype, 12.2 mm; Eight Mile Rock, Grand Bahama; USNM 859316. **Fig. 83.** Paratype, 8.5 mm; Dry Tortugas, Florida; FSBC I 32535. **Fig. 84.** Paratype, 8.1 mm; same lot as 83.



Figs. 85-90. *Acanthochitona roseojugum* Lyons, *sp. nov.* **Fig. 85.** Valve i *ex* 10.0 mm paratype; Eight Mile Rock, Grand Bahama; FSBC I 32537. **Fig. 86.** Valve i *ex* 8.2 mm paratype; Dry Tortugas, Florida; FSBC I 32535. **Fig. 87.** Valve iv, same specimen as 85. **Fig. 88.** Valve iv, same specimen as 86. **Fig. 89.** Valve viii, same specimen as 85. **Fig. 90.** Valve viii, same specimen as 86.

jugum white or pink, suffused on some valves with bright rose spots; girdle white or buff.

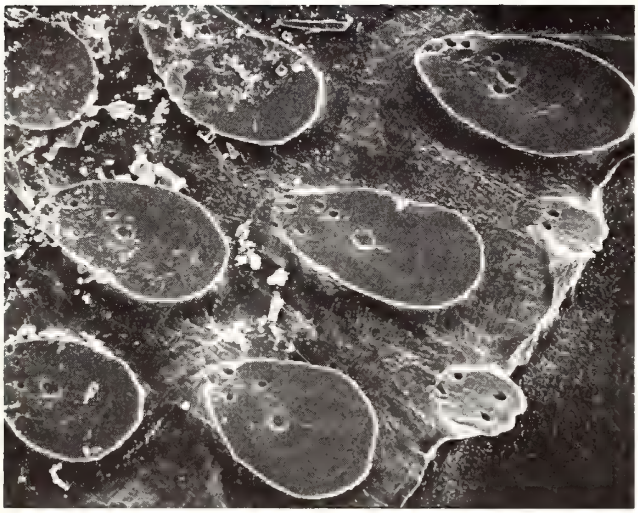
Valve i semilunate (Figs. 85, 86), wider than long, margin straight posteriorly, with anterior insertion plate bearing 5 U-shaped slits; tegmentum occupying 60-65% of valve length. Valves ii-vii beaked posteriorly (Figs. 87, 88); tegmentum subpentagonal, wider than long, with convex to slightly sinuous anterolateral margins; sutural laminae large, flared anterolaterally, with broadly rounded anterior tips separated by broad, U-shaped sinus; single shallow slits along lateral margins. Valve viii with tegmentum subovate (Figs. 89, 90), widest between mucro and anterior margin; mucro elevated, slightly posterior of center; sutural laminae large, broad, subquadrate; 2 small slits in posterior insertion plate.

Jugum elevated, strongly demarked, smooth, narrow, sides parallel, extending anteriorly beyond tegmental margin. Tegmentum of all valves covered with subovate to spatulate, flattened pustules (Figs. 91, 92) 120-140 μm long, 80 μm wide, with single, subcentral macresthete, two pairs of micresthetes, second pair near juncture of apex and tegmental plain.

Girdle upper surface covered with small (40 μm) slender, sharp-tipped spicules; 18 anterior and sutural tufts with 10-18 straight, relatively robust, vitreous spicules 1.25 mm long, surrounded by many similar but smaller (250 μm) spicules; marginal spicules sharp-tipped, vitreous, short (300 μm) anteriorly and laterally, more than twice as long posteriorly; underside covered with fine (80 μm), sharp-tipped, vitreous spicules directed toward periphery.

DISCUSSION: Florida specimens generally have paler color on the tegmentum and girdle, and valves seem to be slightly more protracted. However, the rose spots, extended jugum, and tegmental pustule morphology indicate that Bahamian and Florida populations are conspecific.

Intact specimens of *Acanthochitona roseojugum* hardly seem separable from *A. andersoni* Watters, 1981. Differences useful to sort specimens are almost subjective. Intermediate valves of *A. roseojugum* are wider and more flattened anteriorly, whereas those of *A. andersoni* are more narrow and arched. The jugum of *A. roseojugum* is separated more distinctly from the tegmentum than is that of *A. andersoni.* Rose-colored spots occur on all or part of the jugum of at least valve iii



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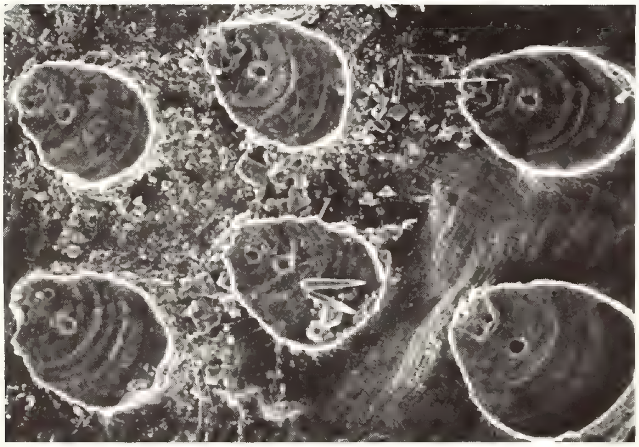

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Figs. 91, 92. *Acanthochitona roseojugum* Lyons, *sp. nov.*, tegmental pustules (field widths = 385 μm). **Fig. 91.** Bahamas; same specimen as 85. **Fig. 92.** Florida; same specimen as 86.

of *A. roseojugum* and sometimes occur on the jugum of all intermediate valves (ii-vii); sutural laminae and undersides of all valves are pink. I have seen two entirely rose-colored specimens of *A. andersoni*, but those specimens were distinguishable by their highly arched, more narrow intermediate valves. Some specimens of *A. pygmaea* from the Bahamas and Puerto Rico are flushed with pale pink on some intermediate valves, but these are immediately separated from *A. roseojugum* by strongly incised grooves on the jugum, wider tegmentum on intermediate valves, smaller sutural laminae, and many green spicules rather than few white spicules in the anterior and sutural tufts.

Any resemblance of *Acanthochitona roseojugum* to *A. andersoni* and *A. pygmaea* is disspelled by inspection of disarticulated valves. The proportionately large insertion plate and small tegmentum of valve i, flared sutural laminae and extended, strongly demarked, smooth jugum of valves ii-viii, and small slits of valve viii all resemble features of species in the *A. hemphilli* complex. However, the straight posterior margin of valve i and the girdle species of *A. roseojugum* differ considerably from those of species in the *A. hemphilli* complex.

The additional asymmetrical slits on insertion plates of valves i and viii of the illustrated Bahamian specimen (Figs. 85, 89) represent anomalies that occur occasionally in many species of *Acanthochitona.*

ETYMOLOGY: From Latin *"roseus"*, rose-colored, and *"iugum"*, a ridge (i.e. jugum).

Acanthochitona balesae **Abbott, 1954**

Figs. 93-104

Acanthochitona balesae Pilsbry, 1940: pl. 12, fig. 5 (*nomen nudum*). Abbott, 1954: 318; 1974: 406. Watters, 1981: 175, 176, pl. 3, figs. a-c.

Acanthochitona elongata Kaas, 1972: 51-53, figs. 90-94, pl. 2, fig. 3. Ferreira, 1985: 212.

Acanthochitona interfissa Kaas, 1972: 53-55, figs. 95-107.

Choneplax lata, Ferreira, 1985: 208-213 (pars) [*non Choneplax lata* (Guilding, 1829)].

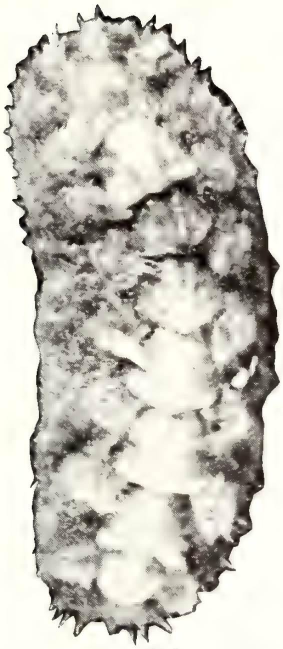
TYPE MATERIAL: HOLOTYPE: *A. balesae:* ANSP 349331 (not examined). *A. interfissa:* 5.5 mm; Monos, Avalon Bay, Trinidad; 10 Jan 1955; RMNH 9092. PARATYPES: *A. interfissa:* TRINIDAD: 1 spec., 7.0 mm; collected with holotype; RMNH 9093. ARUBA: 5 disarticulated intermediate valves; Malmok, Arasji; 14 Aug 1955; RMNH 4502. —1 spec., 8.8 mm; same locality and date; RMNH 9094.

OTHER MATERIAL EXAMINED: FLORIDA: 2 spec., 6.7, 9.6 mm, north side Vaca Key, 0-1 m, 1 Oct 1979, FSBC I 32558. —1 spec., curled, same locality, 4 Aug 1980, FSBC I 32571. —1 spec., 9.2 mm, Bonefish Key, CAS 063327. —1 spec., 9.3 mm, Peanut Id., Palm Beach Inlet, 0-1 m, 17 Aug 1982, FSBC I 30761. —2 spec., 4.4, 6.8 mm, 3 km south of St. Lucie Inlet, 2-3 m, 18 May 1978, IRCZM 61:008. —1 spec., 3.7 mm, same location and date, IRCZM 61:007. BAHAMAS: 1 spec., 8.4 mm, Eight Mile Rock, Grand Bahama, 0.5-1.0 m, 21-23 May 1981, FSBC I 32559. —2 spec., 9.5, 10.6 mm, Bartlett Hill, Eight Mile Rock, 0-0.5 m, 29 Aug 1984, FSBC I 32040. JAMAICA: 1 intermediate valve, Drunkeman's Key, RMNH. ST. EUSTATIUS: 8 spec., 2.4-4.4 mm, Tumble Down Dick Bay, RMNH. TRINIDAD: See type material. VENEZUELA: 1 spec., 7.8 mm, Tortuga Id., CAS 063326. ARUBA: 3 spec., 2.5-8.3 mm, Malmok, 14 Aug 1955, RMNH. —1 spec., 7.0 mm, Seroe Colorado, 2 May 1955, RMNH. —1 spec., 5.1 mm, Rincon, 7 May 1955, RMNH. See also type material. PANAMA: 9 spec., 2.0-4.0 mm, Galeta Id., Canal Zone, Bullock collection. —10 spec., 3.0-5.0 mm, Galeta Id., Bullock collection. —10 spec., 3.0-7.0 mm, Galeta Id., Bullock collection.

TYPE LOCALITY: Bonefish Key (= Fat Deer Key, between Vaca Key and Crawl Key, Monroe County, Florida; see Kaas, 1972) (original designation).

DISTRIBUTION: South Florida and Grand Bahama Island to Caribbean coast of Panama and Trinidad.

DESCRIPTION: Largest specimen 10.6 mm long, 3.7 mm wide including girdle; valves occupying about 33% total specimen width (Figs. 93, 94). Exposed valves white, usually with beige, olive, or brown maculations, occasionally some valves entirely brown-black; intermediate valves noticeably longer than wide.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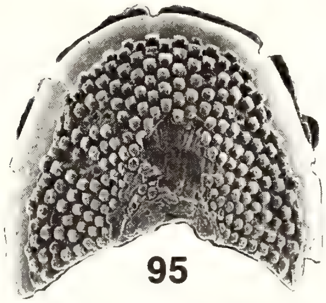
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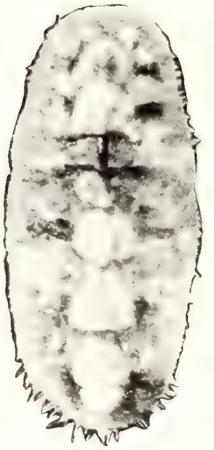
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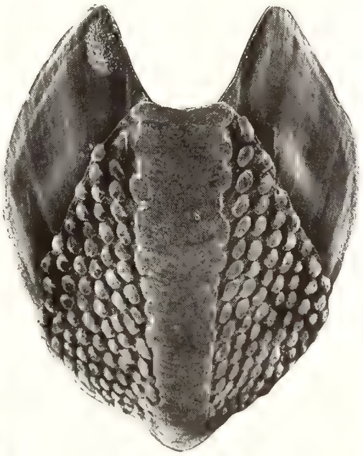
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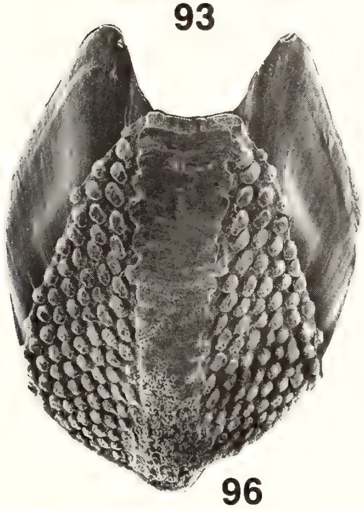
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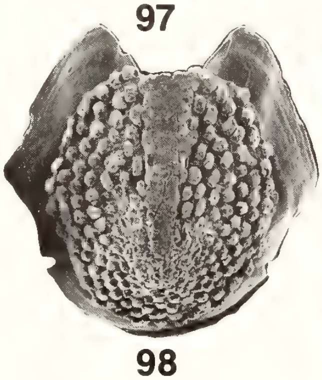
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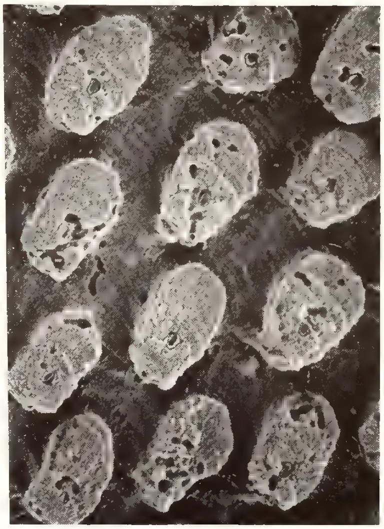
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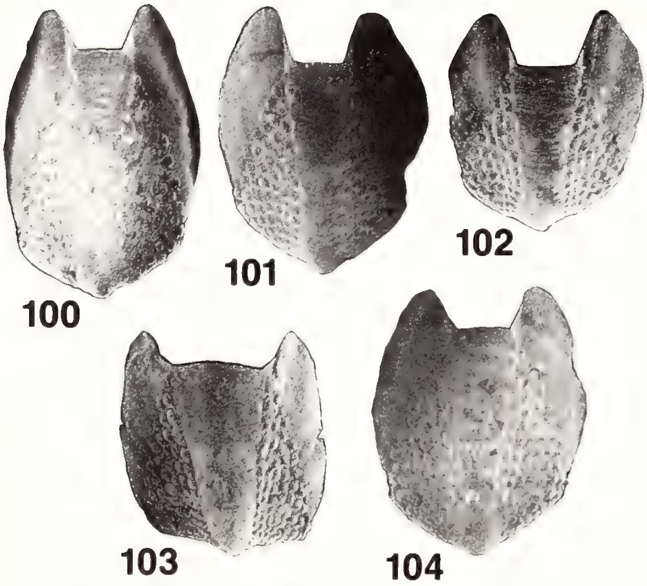
Figs. 93-99. *Acanthochitona balesae* Abbott, 1954. **Fig. 93.** Whole specimen, 9.6 mm; Vaca Key, Monroe County, Florida; FSBC I 32558. **Fig. 94.** Entire specimen, 6.7 mm; same lot. **Fig. 95.** Valve i *ex* curled specimen; Vaca Key, Florida; FSBC I 32571. **Fig. 96.** Valve iv, same specimen. **Fig. 97.** Valve v, same specimen. **Fig. 98.** Valve viii, same specimen. **Fig. 99.** Tegmental pustules, valve iv, same specimen (field width = 240 μm).

Girdle beige to tan (bleached totally white in some preserved specimens), with green, brown, or black patches between white spicule clusters of dorsal tufts.

Valve i semilunate (Fig. 95), slightly wider than long, markedly concave posteriorly, with anterior insertion plate bearing 5 slits; tegmentum occupying about 90% total valve length. Posterior margins of valves iii-vi strongly produced (Figs. 96, 97), those of remaining valves nearly straight; tegmentum longer than wide, subpentagonal, widest at posterolateral corners, with straight anterolateral margins; sutural laminae long, narrow, separated at anterior, acute tips by U-shaped sinus, margins parallel with longitudinal axis of valves, with or without single, narrow slits along margins. Valve viii about as wide as long (Fig. 98), rounded posteriorly, with mucro posterior of center; tegmentum subpentagonal, longer than wide, dropping rapidly behind mucro; sutural laminae long, narrow, with straight anterolateral margins, subacute anterior tips separated by U-shaped sinus; 2 small slits in posterior insertion plate.

Jugum moderately expanded anteriorly, smooth, with irregular lateral margins merging with tegmental pustules. Tegmentum of all valves with peg-like, elevated, ovate to spatulate pustules (Fig. 99) about 90 μm long, 45 μm wide, with single subcentral macresthete, usually 3-4 micresthetes.

Girdle upper surface evenly covered with short (80 μm), straight to slightly bent, blunt or sharp-tipped, light or dark



Figs. 100-104. *Acanthochitona balesae* Abbott, 1954. Intermediate valves of disarticulated paratype of *A. interfissa* Kaas, 1972; Malmok, Arasji, Aruba; RMNH 4502. Length of largest valve (Fig. 100) 1.6 mm, including sutural laminae.

colored spicules; 18 anterior and sutural tufts comprised of about 50 straight, slender, sharp-tipped, vitreous spicules up to 700 μm long; margin fringed with straight, slender, sharp-tipped spicules 250-280 μm long; underside evenly covered with short (50-60 μm), straight, sharp-tipped spicules directed toward periphery.

DISCUSSION: Several names have been proposed for this species. Pilsbry (1940) illustrated without text a chiton he called *Acanthochitona balesae* from Bonefish Key, Florida, thereby creating a *nomen nudum*. Abbott (1954) included *A. balesae* 'Pilsbry 1940' from Bonefish Key, with brief differential diagnostic remarks. Kaas (1972) recognized the nude status of Pilsbry's name; to rectify that problem, he described four specimens from Bonefish Key (RMNH) and named them *A. elongata*. In the same paper, Kaas named *A. interfissa* from Trinidad and Aruba and noted similarities between that species and *A. elongata*. Abbott (1974) included *A. balesae* 'Pilsbry' Abbott, repeated his diagnostic comments, and stated that *A. elongata* was a synonym. Bullock (1974) pointed out that Kaas "overlooked the fact that Abbott ... validated Pilsbry's name, and *A. elongata* Kaas must be considered a junior synonym of *A. balesae* 'Pilsbry' Abbott." Bullock also remarked that the relationship between *A. interfissa* and *A. balesae* should be investigated. Watters (1981) relegated both *A. elongata* and *A. interfissa* to the synonymy of *A. balesae* and designated a lectotype (ANSP 349331; Bonefish Key) for *A. balesae*. Ferreira (1985) incorrectly stated that Abbott (1974) regarded *A. balesae* to be a synonym of *A. elongata*. Ferreira clearly considered Abbott's diagnosis inadequate and without priority over *A. elongata*. He agreed with Watters that *A. interfissa* is a synonym of *A. elongata*, but he also relegated *A. andersoni* Watters, 1981, to the synonomy of *A. elongata*. Finally, Ferreira declared all the above taxa to be juveniles and secondary synonyms of *Choneplax lata* (Guilding, 1829).

The International Code of Zoological Nomenclature requires that, to be available, a species name introduced after 1930 must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon [Article 13(a)(i); ICZN, 1985]. Abbott's (1954) account of *Acanthochitona balesae*, although brief, addressed size, proportions, pustule morphology, shape and ornamentation of the jugum, and a location where the species occurs; some characters were compared with those of *A. pygmaea*. Such treatment satisfies the requirements of ICZN Article 13, so *A. balesae* Abbott, 1954, is valid, and *A. elongata* Kaas, 1972, is a junior synonym.

I examined the holotype and three of the four paratypes of *Acanthochitona interfissa* Kaas and the holotype and seven paratypes of *A. andersoni* Watters. I found no characters upon which to separate the holotype and paratypes of *A. interfissa* from topotypic specimens of *A. balesae* from Bonefish Key, so I cannot refute contentions by Watters (1981) and Ferreira (1985) that *A. interfissa* is a synonym of *A. balesae*. However, *A. andersoni* is not a synonym of *A. balesae*, and neither name is a synonym of *Choneplax lata*.

Several problems are associated with the original description and type series of *Acanthochitona interfissa*. Kaas reported the holotype and a paratype from Trinidad and three paratypes from Aruba. He reported that he disarticulated and illustrated the paratype from Trinidad. However, although the valves and spicules of that specimen now are almost totally dissolved in preservative, the specimen is intact, as is the holotype. One of the Aruba paratypes has been disarticulated. Five of the valves remain (Figs. 100-104), but valves i, viii, and an intermediate valve are missing; none of the valves resembles the curiously misshapen valve ii illustrated by Kaas.

Except for valve viii, the description and illustrations of valves of *Acanthochitona interfissa* (Kaas, 1972: figs. 95-101) seem indistinguishable from those of *A. balesae*. Valve viii of *A. interfissa* as illustrated by Kaas (his figs. 95-97) differs from the corresponding valve of *A. elongata* (= *A. balesae*) (Kaas, 1972: figs. 90, 91) by tegmental shape, pustule configuration and size, jugal length and expansion, by possession of a greatly flared insertion plate and laminae, and most notably, by possession of a medial third slit in the posterior insertion plate. Conversely, valves i, ii, and iv of *A. interfissa* (Kaas, 1972: figs. 98-101) are indistinguishable from those of *A. balesae* whose corresponding valves Kaas described but did not illustrate in the account of *A. elongata* which immediately preceded that of *A. interfissa*.

Ferreira (1985) could have been prompted to combine *Acanthochitona andersoni* with *A. interfissa* because of Kaas' description of valve viii of the latter. Among the Caribbean *Acanthochitona* species, valve viii of *A. interfissa* as illustrated by Kaas most resembles that of *A. andersoni*, if the third slit of *A. interfissa* is ignored. I found a single specimen of *A. andersoni* among three *A. balesae* in an uncatalogued lot (RMNH) from Malmok, Aruba, collected on the same date as were the paratypes of *A. interfissa*. However, no species of *Acanthochitona* normally possesses a third slit in valve viii. Because the 3-slitted valve no longer accompanies the type material, it seems best to regard the third slit as an anomalous, additional one of the kind that sometimes occurs on other normally 2-slitted species.

Kaas (1972) described the sutural laminae of intermediate valves of *Acanthochitona elongata* as "unslit, but with little excavations where the slits might be expected"; for *A. interfissa*, he described "valves with 1 slit, except valves iv-vi which are unslit." The specimen of *A. balesae* I dissected, collected within 1 km of the type-locality, has distinct slits on valves ii and vii but lacks slits on valves iii-vi. Kaas also described a longitudinally striate jugum for *A. elongata*, which he contrasted with the smooth jugum of *A. interfissa*. Although longitudinal striae were sometimes visible beneath the surface, I saw only a smooth jugum on all specimens of *A. balesae* I examined.

Despite my inability to find objective differences between the two taxa, it should be noted that specimens of the northern Caribbean *Acanthochitona balesae* and those of the southern *A. interfissa* can be sorted by seemingly subjective characters. Basically, southern specimens are smaller, more drab, and have finer spicules and sculpture than northern specimens. Using those "characters", all Florida and Bahamian specimens are assignable to *A. balesae* and all specimens from St. Eustatius to Trinidad, Venezuela, Aruba and Panama are assignable to *A. interfissa*. Further work may yet reveal objective characters which can be used to demonstrate two species within the group.

Watters' (1981) drawings of valves from Puerto Rico are too schematic to reveal with certainty whether they belong to *A. balesae*.

Acanthochitona andersoni Watters, 1981

Figs. 105-109

Acanthochitona andersoni Watters, 1981: 173-176, pl. 2e-g, pl. 4i.

Acanthochitona pygmaea, Lyons, 1981: 36 (pars, Dry Tortugas sta. 4 only) [*non A. pygmaea* (Pilsbry, 1893)].

Choneplax lata, Ferreira, 1985: 208-213 (pars) [*non C. lata* (Guilding, 1829)].

TYPE MATERIAL: HOLOTYPE: 11.3 mm, Calliagua, St. Vincent, Feb 1972, ANSP 332171. PARATYPES: FLORIDA: 1 spec., 6.4 mm, off Destin, 55 m, ANSP 220834. —2 spec., 5.7, 7.5 mm, West Summerland Key, Oct 1973, Bullock collection. —1 spec., curled, West Summerland Key, 1 June 1974, Bullock collection. —1 spec., 5.3 mm, off Boynton, 55 m, ANSP 220833. BAHAMAS: 1 spec., 9.5 mm, west of Haulover, North Bimini, ANSP 325808. —1 spec., 7.5 mm, east of Turtle Rocks, 6 m, ANSP 325864.

OTHER MATERIAL EXAMINED: FLORIDA: 1 spec., 5.7 mm, Garden Key, Dry Tortugas, 0-2 m, 5 Oct 1979, FSBC I 32551. —3 spec., 4.6-7.5 mm, Garden Key, 30 Apr 1975, CAS 063329. —1 spec., 6.3 mm, Key West, CAS 063321. —1 spec., 11.5 mm, West Summerland Key, 1976, Bullock collection. —1 spec., curled, West Summerland Key, 1978, Bullock collection. —1 spec., 8.0 mm, Missouri Key, 0.5-1.0 m, 25 July 1987, FSBC I 32557. —1 spec., curled, Burnt Point, Crawl Key, 2.5 m, 4 Aug 1982, FSBC I 32426. —1 spec., 4.7 mm, Tennessee Reef, off Long Key, 13.7 m, 12 July 1986, FSBC I 32556. —1 spec., 7.0 mm, Elbow Reef, 25°07.7'N, 80°15.9'W, 18.3 m, 7 June 1979, IRCZM 61:018. —3 spec., curled, east of Elliott Key, RMNH. —1 spec., 8.8 mm, Peanut Id., Palm Beach Inlet, 0-1 m, 29 Aug 1982, FSBC I 30762. BAHAMAS: 2 spec., 3.4, 10.1 mm, Bartlett Hill, Eight Mile Rock, Grand Bahama, 0-0.5 m, 29 Aug 1984, FSBC I 32553. —1 spec., 7.5 mm, Tamarind Beach Reef, Grand Bahama, 18 m, 28 Aug 1984, FSBC I 32552. —2 spec., 7.2, 8.0 mm, Green Turtle Cay, Abaco, 0.5 m, May 1978, FSBC I 32550. PUERTO RICO: 1 spec., 6.0 mm, Isla Turramote, La Parguera, May 1985, FSBC I 32554. SABA: 5 spec., curled, Fort Bay pier, 7 July 1973, RMNH. ST. LUCIA: 2 spec., 8.0, 9.0 mm, Anse Chastenet, 1-3 m, 4 Nov 1984, Bullock collection (1), FSBC I 32572 (1). ARUBA: 1 spec., 3.0 mm, Malmok, Arasji, 14 Aug 1955, RMNH. BONAIRE: 1 spec., 9.0 mm, 2 km north of Kralendijk, 4 m, 7 Oct 1986, FSBC I 32555. CURAÇAO: 1 spec. (?), 2.0 mm, Piscadera Baai, 0-4 m, Apr 1966, Bullock collection. —1 spec. (?), 2.5 mm, Knip Baai, 6 Feb 1949, RMNH. VENEZUELA: 1 spec., crushed, Tortuga Id., 1 Aug 1936, RMNH.

TYPE LOCALITY: Calliagua, St. Vincent (original designation).

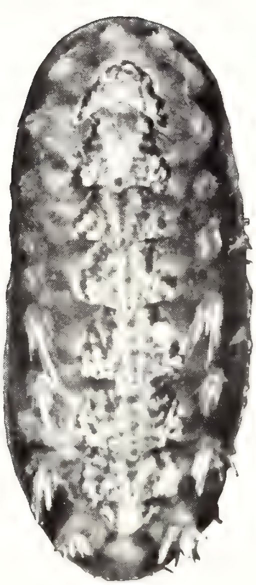
DISTRIBUTION: Both coasts of Florida, the Bahama Islands, the Lesser Antilles, southern Netherlands Antilles, and Venezuela. Watters (1981) also reported specimens from Quintana Roo, Mexico, and Caribbean Panama.

DESCRIPTION: Largest specimen (holotype) 11.3 mm long, 4.8 mm wide including girdle; valves occupying about 50% of total specimen width (Fig. 105). Exposed parts of valves of holotype white, extensively mottled with black; most other specimens white or light green with few brown or black flecks, few specimens apricot or rose. Girdle white, buff, tan, or dark brown, often with bar-like maculations; spicules translucent white.

Valve i semilunate (Fig. 106), wider than long, slightly to markedly concave posteriorly, with anterior insertion plate bearing 5 slits; tegmentum occupying 70-75% total valve length. Valves ii-vii prominently beaked posteriorly (Fig. 107); tegmentum pentagonal, as wide or wider than long, with slightly convex anterolateral margins; sutural laminae moderately to considerably produced anteriorly, with vague to distinct anterolateral angle, subacutely rounded anteriorly, separated by wide anterior sinus; single slits along lateral margins. Valve viii pentagonal (Fig. 108), widest at anterolateral corners, dropping away rapidly behind elevated, postcentral mucro; sutural laminae well-developed, with straight margins and sharply angled corners; 2 narrow, relatively small slits in posterior insertion plate.

Jugum smooth, narrow, little expanded anteriorly, merging laterally with tegmental pustules. Tegmentum of all valves covered with ovate or subspatulate pustules (Fig. 109) 90-130 μm long, 60-80 μm wide, with single adapical macresthete, 2-6 micresthetes between macresthete and apex.

Girdle upper surface covered with dense mat of very small (40 μm) slender spicules; 18 anterior and sutural tufts comprised of 12-20 stout, straight, sharp-tipped vitreous spicules up to 1.2 mm long, accompanied at base by many sharp, slender, needle-like spicules about 200 μm long; margin fringed with stout, straight to slightly curved vitreous spicules about 140 μm long, with markedly larger (200 μm) but other-



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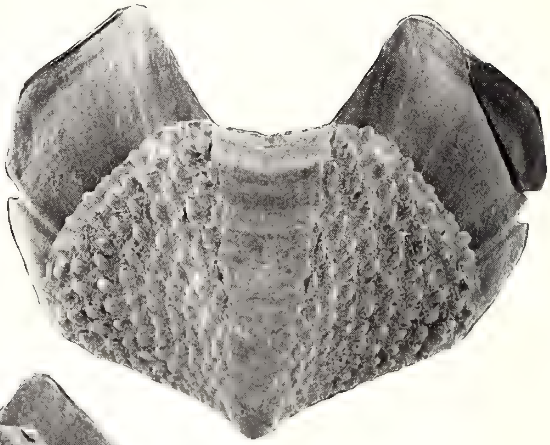

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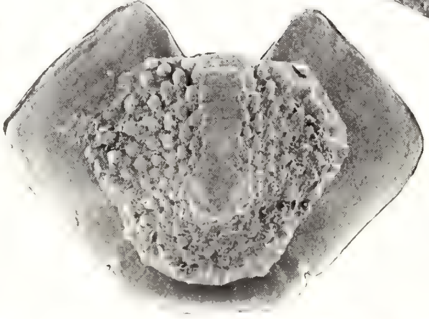

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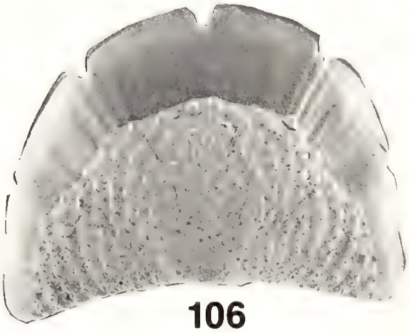

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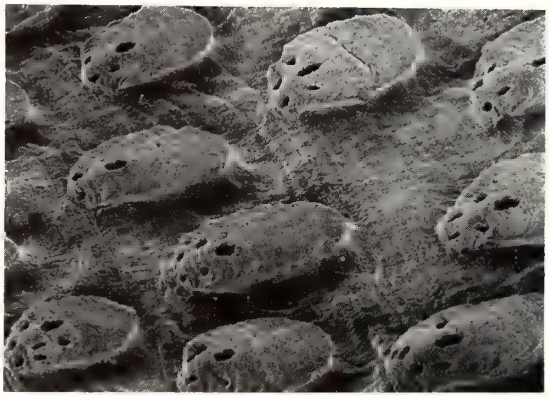

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Figs. 105-109. *Acanthochitona andersoni* Watters, 1981. **Fig. 105.** Holotype, 11.3 mm; Calliagua, St. Vincent; ANSP 332171. **Fig. 106.** Valve i *ex* 8.0 mm specimen; Anse Chastenet, St. Lucia; FSBC I 32572. **Fig. 107.** Valve iv, same specimen. **Fig. 108.** Valve viii, same specimen. **Fig. 109.** Tegmental pustules, valve iv *ex* 8.0 mm specimen; Green Turtle Cay, Abaco, Bahamas; FSBC I 32550 (field width = 365 μm).

wise similar spicules sparsely scattered throughout; underside covered with slender, sharp-tipped, vitreous spicules about 80 μm long directed toward periphery.

DISCUSSION: Specimens of *Acanthochitona andersoni* have been confused with *A. pygmaea, A. balesae,* and *Choneplax lata.* The smooth, not incised jugum and relatively narrow, not widely rectangular intermediate valves distinguish *A. andersoni* from *A. pygmaea.* The tegmentum of intermediate valves of *A. andersoni* is as wide or slightly wider than long, whereas that of *A. balesae* is longer than wide. Morphology of tegmental pustules is also distinctive for each of the three species. *A. andersoni* is not *C. lata*, as evidenced by possession of 2 distinct slits on valve viii. Ferreira (1985) identified lots CAS 063329 from Dry Tortugas and IRCZM 61:108 from Elbow Reef as *Choneplax lata* and CAS 063321 from Key West as *Acanthochitona spiculosa.*

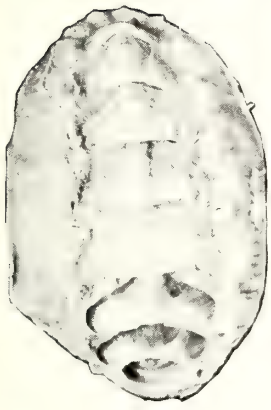
Acanthochitona bonairensis Kaas, 1972

Figs. 110-113

Acanthochitona bonairensis Kaas, 1972: 44, 45, figs. 72, 73, pl. 3, figs. 1, 2. Ferreira, 1985: 207, 214.
Acanthochitona communis, Watters, 1981: 173.
Acanthochitona fascicularis, Kaas, 1985: 586.

TYPE MATERIAL: HOLOTYPE: 33 mm x 22 mm, Bonaire, RMNH.

DISCUSSION: Nothing can be added to the original description. Kaas (1972) noted the similarity in valve morphology between *Acanthochitona bonairensis* and the European species *A. communis* (Risso, 1826), but also described considerably shorter, more delicate girdle spicules on *A. bonairensis* than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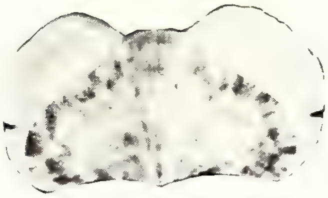
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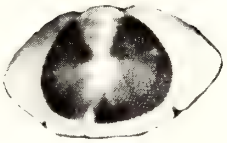
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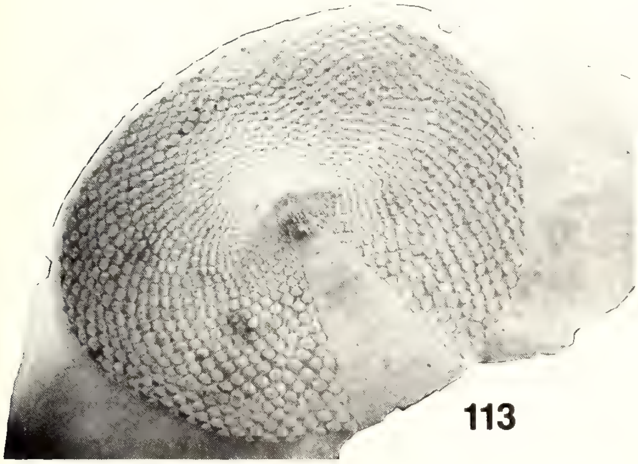
Figs. 110-112. *Acanthochitona bonairensis* Kaas, 1972. **Fig. 110.** Holotype, 33.0 mm; Punt Vierkant, Bonaire; RMNH. **Fig. 111.** Valve vii of holotype. **Fig. 112.** Valve viii of holotype.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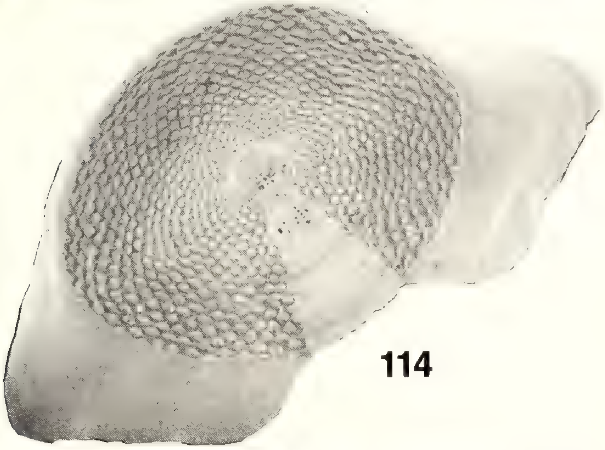
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Fig. 113. *Acanthochitona bonairensis* Kaas, 1972. Valve viii of holotype. **Fig. 114.** *Acanthochitona fascicularis* (Linné, 1767). Valve viii *ex* specimen from Roscoff, France; FSBC I 32427. Compare outline of tegmentum with that of specimen in Fig. 113.

on *A. communis.* Watters (1981) ignored the described differences and declared *A. bonairensis* to be a synonym of *A. communis.* Kaas (1985) followed that synonymy in his review of *A. fascicularis* (Linné, 1767), a senior synonym of A. *communis.* However, Ferreira (1985) retained *A. bonairensis* as one of the few Caribbean species he considered distinct.

I compared the holotype of *Acanthochitona bonairensis* (Figs. 110-112) with specimens of *A. fascicularis* from Roscoff, France (FSBC I 32427). Differences in valve morphology (Figs. 113, 114) noted by Kaas (1972), although subtle, were confirmed, as were marked differences in girdle spicules. *A. bonairensis* remains known only from the holotype. Discovery of more Caribbean specimens would help considerably in interpretation of differences noted to date. Until such specimens are found, I believe the differences in girdle spicules provide sufficient reason to maintain *A. bonairensis* as a Caribbean species distinct from the European *A. fascicularis.*

Acanthochitona zebra Lyons, *sp. nov.*

Figs. 115-127

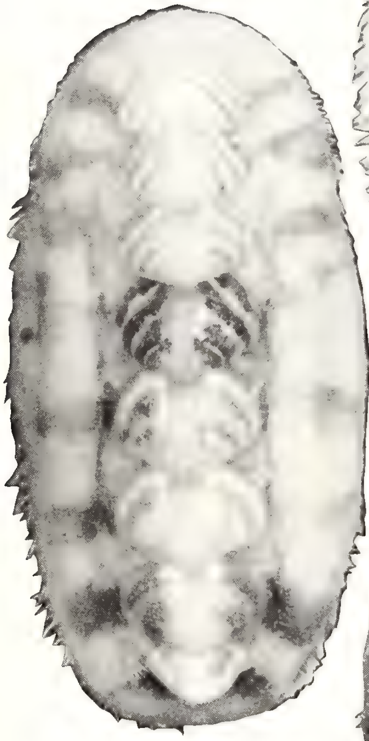
(?) *Choneplax lata,* Kaas, 1972: 55-58, figs. 108-116, pl. 2, fig. 4 (pars) [*non C. lata* (Guilding, 1829)].
Acanthochitona sp. Lyons, 1981: 35, 36.
Choneplax lata, Ferreira, 1985: 208-213 (pars). [*non C. lata* (Guilding, 1829)].

TYPE MATERIAL: HOLOTYPE: Length 15.0 mm, Silver Cove Canal, Freeport, Grand Bahama Island, 0.5-1.5 m, 28 Aug 1984, W. G. Lyons, collector, USNM 859319. PARATYPES: FLORIDA: 1 spec., 12.0 mm, Long Key Reef, Dry Tortugas, intertidal, 11-12 May 1979, FSBC I 32479. —6 spec., 7.0-11.2 mm, patch reef near Long Key Reef, Dry Tortugas, 1.5-2.5 m, 11-12 May 1979, ANSP A12125 (1), FSBC I 32478 (5). —1 spec., 4.5 mm, Tennessee Reef, off Long Key, 13.7 m, 12 July 1986, FSBC I 32485. BAHAMAS: 1 spec., 11.3 mm, same locality and date as holotype, FSBC I 32483. —1 spec., 9.7 mm, Caravel Beach, Freeport, Grand Bahama, 1 m, Jan 1981, FSBC I 32480. —6 spec., 5.0-10.0 mm, Tamarind Beach Reef, Grand Bahama, 18 m, 28 Aug 1984, RMNH 55990 (1), FSBC I 32482 (5). — 1 spec., 8.2 mm, Salt Pond, Long Island, Aug 1975, CAS 063328. PUERTO RICO: 2 spec., 7.2, 9.3 mm, Isla Turramote, La Parguera, 9.1 m, May 1985, FSBC I 32484. BELIZE: 1 spec., 15.0 mm, Carrie Bow Cay, 0-1 m, 23 Mar 1981, IRCZM 61:092.

OTHER MATERIAL EXAMINED: FLORIDA: 1 spec., 3.4 mm, east of Elliott Key, 2-6 m, 5 Sept 1963, RMNH. BAHAMAS: 7 intermediate valves, Gold Rock, Grand Bahama, bottom sediments, 24.4 m, May-July 1981, FSBC I 32481. —7 intermediate valves, Grand Bahama, bottom sediments, May 1981, R. Quigley collection. ARUBA: 2 spec. (?), both small, missing valve viii, Paardenbaai rif, 28 Apr 1955, RMNH. CURAÇAO: 3 spec., 5.2-7.3 mm, Piscadera Baai, 27 July 1973, RMNH. —2 spec. (?), 2.7, 2.9 mm, Caracas Baai, 22 Apr 1955, RMNH. —1 spec., 6.5 mm, Spaanse Water, 17 Nov 1968, RMNH. —1 spec. (?), 3.4 mm, Awa di Oostpunt, 0.25-1.0 m, 22 Feb 1970, RMNH.

TYPE LOCALITY: Silver Cove Canal, Freeport, Grand Bahama Island.

DISTRIBUTION: Dry Tortugas, Florida Keys, and Grand Bahama Island to Puerto Rico and Belize, Aruba and Curaçao; intertidal to 18 m, single valves from sediments in 24.4 m.



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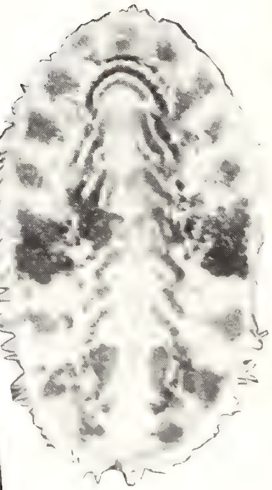

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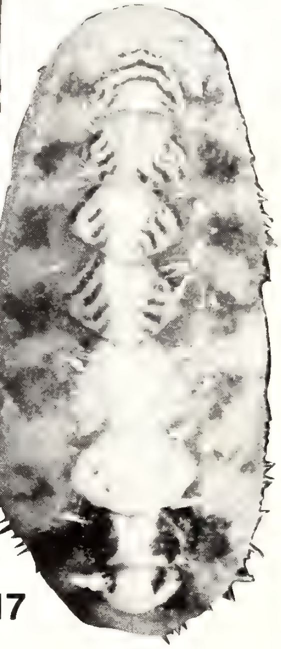

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Figs. 115-117. *Acanthochitona zebra* Lyons, *sp. nov.* **Fig. 115.** Holotype, 15.0 mm; Freeport, Grand Bahama; USNM 859319. **Fig. 116.** Paratype, 8.3 mm; Tamarind Beach Reef, Grand Bahama; FSBC I 32482. **Fig. 117.** Paratype, 11.1 mm; Dry Tortugas, Florida; FSBC I 32478.

DESCRIPTION: Largest specimen (holotype) 15.0 mm long, 7.2 mm wide including girdle; valves and girdle occupying approximately equal portions of total specimen width (Figs. 115-117). Valve i with 3-5 olivaceous or brown concentric bands, expressed on valves ii-vii as transverse stripes (chevrons) extending posterolaterally from jugum; bands usually strongest on valves i-v, commonly obscured by overall dark olive or brown color on valves iv and vii; valve viii mostly white, with single large olivaceous spots on lateral areas. Girdle white with irregular olivaceous or green bands crossing upper surface from valves to peripheral margins, sometimes with broad, black spots at middle or elsewhere on each side.

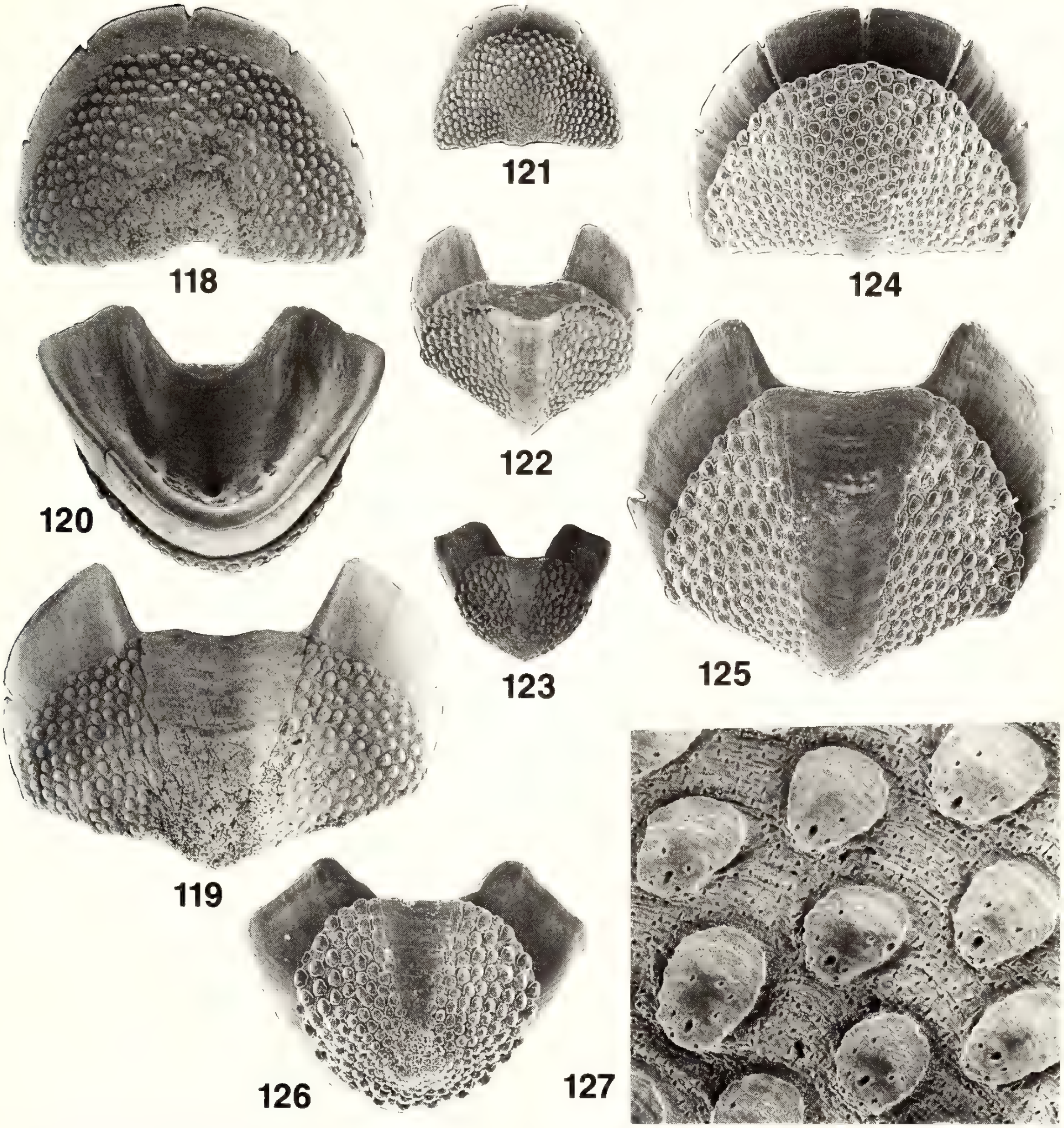
Valve i semilunate (Fig. 118), wider than long, posterior margin straight, slightly beaked, with anterior insertion plate bearing 5 slits; tegmentum occupying 80-85% of valve length. Valves ii-vii strongly beaked posteriorly (Fig. 119); tegmentum evenly to broadly pentagonal, with convex anterolateral margins; sutural laminae moderately narrow, curving anteromedially from posterolateral corners of tegmentum, with subacute anterior tips separated by broad sinus of same width as anterior end of jugum; single narrow slits along lateral margins. Valve viii tegmentum roughly ovate, widest mesially, truncate anteriorly, extending to overhang posterior edge of insertion plate (Fig. 120). Mucro distinctly posterior; sutural laminae extending obliquely anteriorly, subquadrate, of moderate length; two slits in posterior insertion plate very fine, barely discernible with dissecting microscope. Valve morphology of Puerto Rican juveniles and Floridan adults as illustrated (Figs. 121-126).

Jugum of valves ii-viii smooth, wedge-shaped, widest anteriorly. Tegmentum covered with densely packed, flattened, spatulate pustules (Fig. 127), approximately 80-100 μm long, 70 μm wide, radiating anteriorly from beak of valve i, anterolaterally from jugum of valves ii-vii, and from mucro of valve viii; pustules with single macresthete near apex, 4-7 micresthetes surrounding macresthetes, sometimes more on Florida specimens; many additional micresthetes dispersed across surface of tegmental plain.

Girdle upper surface covered with fine (100 μm) spicules; 18 anterior and sutural tufts comprised of 8-10 reddish brown, amber, or white, moderately long (to 650 μm), slightly curved, blunt-tipped spicules; marginal spicules straight or slightly curved, approximately 550 μm long, with blunt tips, white, sometimes alternating with amber; underside covered with fine (60 μm), sharp-tipped spicules directed toward periphery.

DISCUSSION: The olivaceous stripes on the tegmentum of *Acanthochitona zebra* strongly resemble those of *A. lineata*, and *A. astrigera* sometimes has white stripes or maculations on the dark blue-green tegmentum of some valves. Moreover, all three species occurred together at the type-locality of *A. zebra*. However, *A. zebra* can be separated readily from the other two species by its extremely posterior mucro, from which the tegmentum drops rapidly to overhang the posterior insertion plate, and by the dorsal tufts of the girdle, which contain only 8-10 blunt-tipped spicules. Pustular shape, as well as location of macrestheses and micresthetes, further distinguish *A. zebra* from *A. astrigera* and *A. lineata.*

Valve proportions of Florida specimens differ somewhat from those of specimens from the Bahamas and Puerto Rico, but morphology of valve viii and the tegmental pustules, as well as the color pattern, indicate they are conspecific. Five RMNH lots from Aruba and Curaçao appear to be this species, but the concentric bands and stripes are only weakly expressed on the four largest (5.2-7.3 mm) specimens and are not evident at all on the five smaller (2.7-3.4 mm) specimens.



Figs. 118-127. *Acanthochitona zebra* Lyons, *sp. nov.* **Fig. 118.** Valve i *ex* 10.0 mm paratype; Tamarind Beach Reef, Grand Bahama; FSBC I 32482. **Fig. 119.** Valve iv, same specimen. **Fig. 120.** Valve viii, same specimen; ventral view showing underhung posterior insertion plate with vestigial slits. **Fig. 121.** Valve i *ex* 7.2 mm paratype; Isla Turramote, Puerto Rico; FSBC I 32484. **Fig. 122.** Valve iv, same specimen. **Fig. 123.** Valve viii, same specimen. **Fig. 124.** Valve i *ex* 11.0 mm paratype; Dry Tortugas, Florida; FSBC I 32478. **Fig. 125.** Valve iv, same specimen. **Fig. 126.** Valve viii, same specimen. **Fig. 127.** Tegmental pustules, valve iv, same specimen as 118 (field width = 335 μm).

Ferreira (1985) identified the CAS specimen from Long Island, Bahamas, and the IRCZM specimen from Carrie Bow Cay, Belize, as *Choneplax lata*.

ETYMOLOGY: From the Amharic *"zebra"*, as in *Equus zebra*, an African equine with similar markings.

Genus *Choneplax* Dall, 1882
Choneplax lata (Guilding, 1829)

Figs. 128-145

Chitonellus latus Guilding, 1829: 28.
Chiton strigatus Sowerby, 1840: 289.
(?)*Chiton hastatus* Sowerby, 1840: 290, pl. 16, fig. 4.
Choneplax latus, Pilsbry, 1893: 60, pl. 8, fig. 15.
Choneplax lata, Kaas, 1972: 55-58, figs. 108-116, pl. 2, fig. 4 (pars). Ferreira, 1985: 208-213 (pars).

MATERIAL: BAHAMAS: 4 spec., large, curled, West End, Grand Bahama, intertidal, May 1977, FSBC I 32546. —3 spec., 17.7-22.4 mm, Settlement Point, West End, Grand Bahama, 2 m, 23 May 1981, FSBC

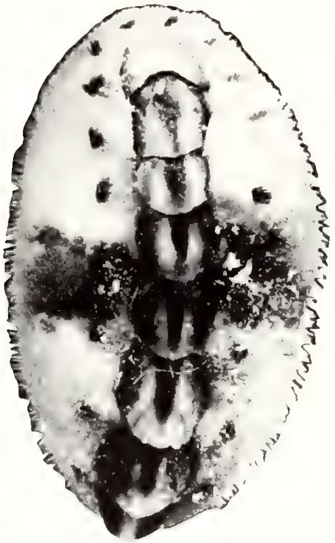
I 32547. —55 spec., 6.5-32.0 mm, Bahama Beach Canal, West End, Grand Bahama, intertidal, 29 Aug 1984, FSBC I 32548. —1 spec., 26.0 mm, New Providence, CAS 063325. —1 spec., 15.0 mm, Nicolls Town, Andros, 2 m, July 1976, CAS 063323. CUBA: 2 spec., 15.9, 17.0 mm, Phillips Park, Guantanamo Bay, intertidal, 9 Apr 1984, FSBC I 32549. BELIZE: 3 spec., 19.0-22.0 mm, Carrie Bow Cay, 0-1 m, 23 Mar 1981, IRCZM 61:051. —1 spec., 9.0 mm, same locality and date, IRCZM 61:053. HONDURAS: 1 spec., 10.0 mm, First Bight, Roatan, 1-2 m, Aug 1982, FSBC I 32073. GUADELOUPE: 4 spec., 13.0-20.0 mm, Guadeloupe, 28 May 1978, CAS 063324.

TYPE LOCALITY: St. Vincent (original designation).

DISTRIBUTION: Grand Bahama Island, Cuba, Belize, Honduras, Guadeloupe, St. Vincent; intertidal and shallow (1-2 m) subtidal zones. Kaas (1972) reported specimens from the Virgin Islands, Tobago, Bonaire, and Curaçao.

DESCRIPTION: Largest specimen 32.0 mm long, 13.7 mm wide including girdle; valves occupying approximately 33% of total specimen width (Fig. 128), proportionally more in juveniles (Fig. 129). Valves brown-black, frequently eroded to create bluish white bands between jugum and lateral margins. Girdle yellow to greenish gold, often with brown or black band across middle.

Valve i semilunate (Fig. 130), wider than long, slightly sinuous posteriorly, with anterior insertion plate bearing 5 distinct slits which continue as shallow grooves leading to anterior edge of tegmentum; tegmentum occupying approx-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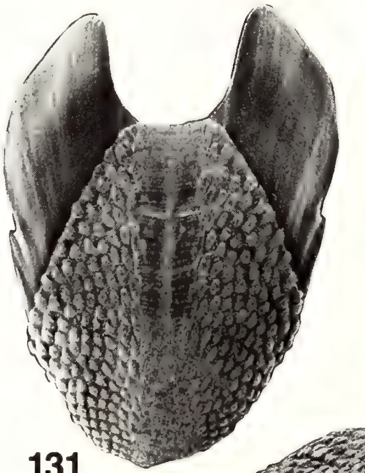
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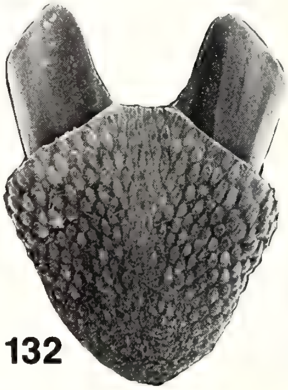
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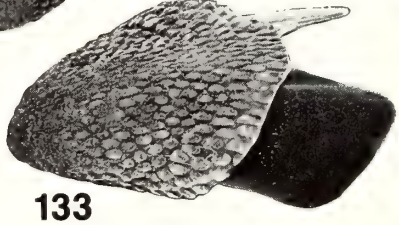
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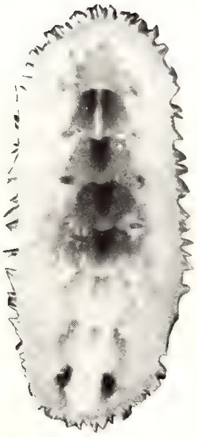
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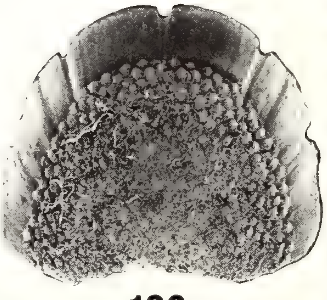
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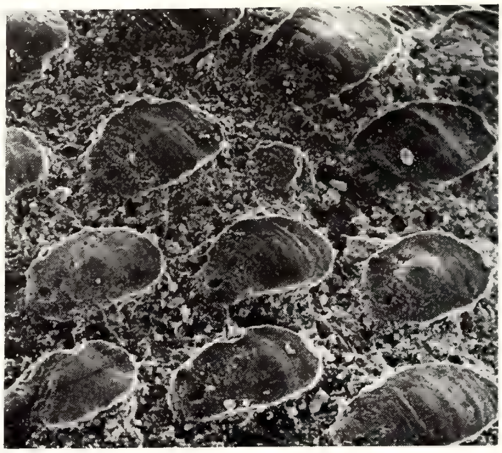
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Figs. 128-134. *Choneplax lata* (Guilding, 1829). **Fig. 128.** Whole specimen, 22.4 mm; Settlement Point, Grand Bahama; FSBC I 32547. **Fig. 129.** Juvenile, 6.5 mm; West End, Grand Bahama; FSBC I 32548. **Fig. 130.** Valve i *ex* 13.0 mm specimen; same lot as 129. **Fig. 131.** Valve iv, same specimen. **Fig. 132.** Valve viii, same specimen, dorsal view. **Fig. 133.** Same valve viii, lateral view. **Fig. 134.** Tegmental pustules, valve iv, same specimen (field width = 315 μm).

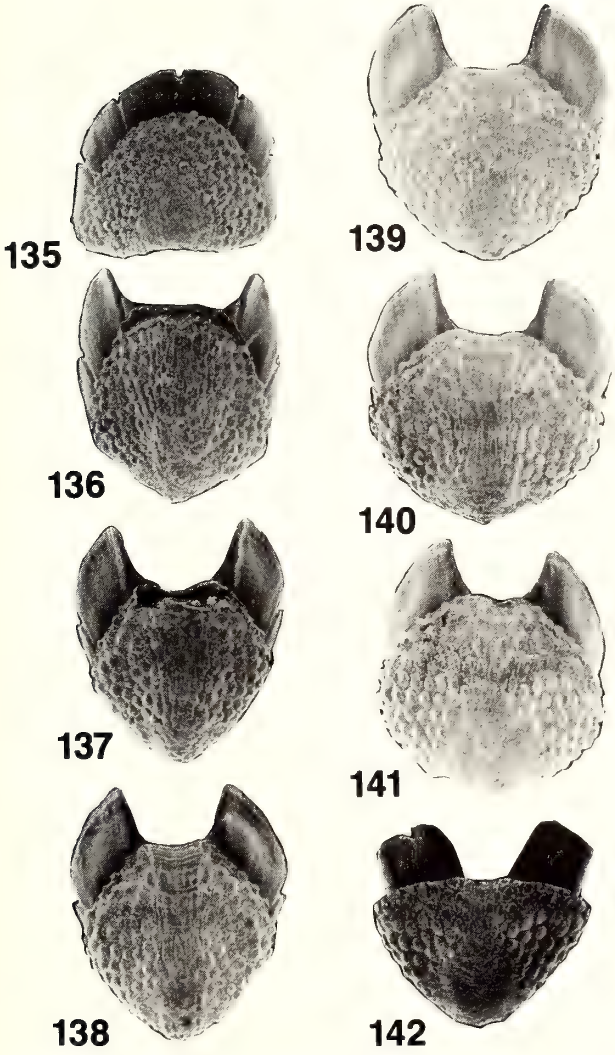
imately 85% of valve length. Valves ii-vii elongate (Fig. 131), strongly produced posteriorly to overhang following valves; tegmentum elongate, pentagonal, widest behind middle, with straight anterolateral margins; sutural laminae long, nearly in line with plane of valves, curving anteromedially from posterolateral corners of tegmentum, with subacute tips separated anteriorly by deep, U-shaped sinus; single, shallow, notch-like slits along lateral margins. Valve viii tegmentum pentagonal (Fig. 132), widest anteromesially, produced posteriorly, with mucro at posterodistal tip (Fig. 133); jugum absent; sutural laminae extending tooth-like from anterolateral margins of tegmentum; posterior insertion plate and slits absent. Tegmental morphology of small specimens varies considerably from that of larger specimens (Figs. 135-142). Valves of very large specimens usually so eroded that posterior edges are straight instead of pointed.

Jugum of valves ii-vii smooth, relatively narrow, little expanded anteriorly; jugum indistinct on valves of small specimens. Tegmentum of all valves covered evenly with coarse, spatulate pustules (Fig. 134) approximately 90 μm long, 50 μm wide, generally flattened but with raised, central dome and adapical macresthete, few or no micresthetes.

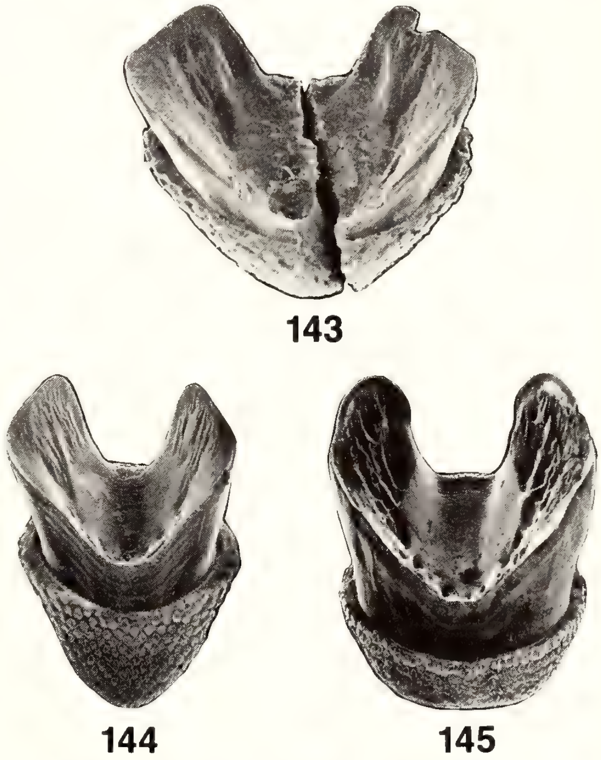
Girdle upper surface covered with small (100 μm), densely packed, club-shaped spicules; anterior and sutural tufts poorly developed, comprised of about 18-22 short (to 1.0 mm), stout, smooth, sharp-tipped, reddish brown or sometimes white spicules; marginal spicules 500 μm long, smooth, straight or slightly curved, white, rarely reddish brown; underside covered with small (100 μm), straight, sharp-tipped, clear spicules.

DISCUSSION: *Choneplax lata* is distinguished from all species of *Acanthochitona* by lacking slits on the posterior margin of valve viii (Figs. 143-145). Kaas (1972) and Ferreira (1985) discussed uncertainty regarding the number of slits on valve i and intermediate valves. The three specimens I dissected (6.7-30.0 mm) each had 5 distinct slits on valve i, not 3 as reported by Pilsbry (1893), and single, notch-like slits on intermediate valves. Based on the 5-slitted valve i, *Choneplax* is more similar to *Acanthochitona* than to *Cryptoplax*, which has 3 slits; however, *Choneplax* shares the unslit tail valve with *Cryptoplax*.

Chiton strigatus Sowerby, 1840, has long been



Figs. 135-142. *Choneplax lata* (Guilding, 1829). Valves i-viii *ex* 6.7 mm juvenile; West End, Grand Bahama; FSBC I 32548.



Figs. 143-145. *Choneplax lata* (Guilding, 1829). Valves viii, ventral views. **Fig. 143.** 6.7 mm specimen, same as Fig. 142 (specimen cracked during handling). **Fig. 144.** 13.0 mm specimen, same as Fig. 132. **Fig. 145.** *Ex* approximately 30.0 mm specimen (curled); West End, Grand Bahama; FSBC I 32546.

recognized as a later name for *Choneplax lata*. Status of *Chiton hastatus* Sowerby, 1840, is less certain; most of the described characters seem to indicate relationship to *Choneplax*, but Carpenter (*In* Pilsbry, 1893) examined the type specimen and reported 2 slits in valve viii, indicating a species of *Acanthochitona*.

Even though valve morphology changes considerably with growth, *Choneplax lata* specimens of all sizes can be recognized readily. Consequently, Kaas' (1972) illustrations of *C. lata* are perplexing. Drawings of a specimen from St. John, Virgin Islands (Kaas figs. 108-112: "9 x 6.5 mm, curled") depict a valve iv considerably wider than long, with short sutural laminae, and a valve viii with a jugum and with lateral margins of relatively short sutural laminae flush with those of the tegmentum, which is posteriorly truncate. Although the unslit insertion plate seems identical to that of *C. lata*, other illustrated features differ markedly from valves iv and viii of the 6.7 and 13.0 mm specimens from Grand Bahama illustrated here (see Figs. 131, 132, 138, 142, 143, 144). I did not illustrate dorsal views of valves from larger specimens because they inevitably were eroded. However, I did dissect a large specimen; most valves were posteriorly truncate but, except for valve ii, the sutural laminae were relatively longer, not shorter, than those of valves illustrated, and the tegmentum was always longer than wide.

Kaas' photograph (1972: pl. 2, fig. 4), reportedly of a 10.5 mm dried specimen of *Choneplax lata* from Spaanse Water, Curaçao, is difficult to interpret but does not much resemble *C. lata*. I did not examine any of the specimens Kaas reported from the Virgin Islands, Tobago, Bonaire, or Piscadera Baai and Spaanse Water, Curaçao. However, I did examine five uncatalogued RMNH lots of small specimens (2.7-7.3 mm) labeled *C. lata* from Aruba and Curaçao, including Piscadera Baai and Spaanse Water. Those lots all contained specimens of *Acanthochitona zebra*, a species which resembles *C. lata* in the number, color, and shape of dorsal tuft spicules and by the underhung insertion plate of valve viii. Kaas also reported only small specimens (4-11 mm), and characters he described on specimens from Bonaire and Curaçao could apply as well to *A. zebra* as to *C. lata*. I am not certain that specimens of both species were not mixed in his account.

Ferreira (1985) ascribed greater morphological variation to small specimens of *Choneplax lata* than actually exists. Inexplicably, he decided that *Acanthochitona andersoni, A. balesae,* and *A. interfissa* were juveniles of *C. lata*. That conclusion was incorrect, as demonstrated in preceding treatments of those taxa. A simple proof, in addition to described differences, is obtained by comparing valves viii. All of the above *Acanthochitona* species, regardless of size, have 2 slits and an obvious jugum on valve viii, whereas even very small (6.7 mm length) *C. lata* lack any indications of posterior slits or a jugum.

Ferreira's confusion renders his distributional records of *Choneplax lata* unreliable. Among IRCZM and CAS specimens he identified, I found specimens of *Acanthochitona andersoni, A. balesae,* and *A. zebra* as well as true *C. lata*. The illustrated specimen he tentatively labeled *Choneplax* cf. *lata* from Barbados appears to be *A. worsfoldi*. Those discrepancies are noted in the appropriate species accounts, but many more lots must be re-examined before all of the records can be corrected.

There seems to be no valid record of *Choneplax lata* from Florida, perhaps because acceptable habitat does not occur there. Specimens I collected at three locations in Grand Bahama and Cuba lived along high energy rocky shores washed by oceanic waves. Pilsbry (1893) described specimens of *C. lata* as vermiform, an apt descriptor considering their tendency to live in small round holes bored into large limestone rocks.

Genus *Cryptoconchus* Burrow, 1815

Cryptoconchus floridanus (Dall, 1889)

Figs. 146-149

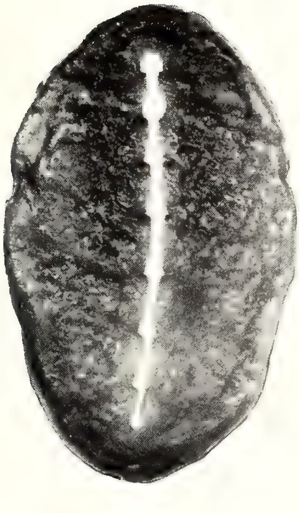
Notoplax floridanus Dall, 1889b: 416.
Acanthochites (Cryptoconchus) floridanus, Pilsbry, 1893: 37, 38, pl. 3, figs. 63, 64.
Cryptoconchus floridanus, Thiele, 1910: 110. Kaas, 1972: 34-36, figs. 55-57, pl. 1, figs. 4, 5.

MATERIAL EXAMINED: FLORIDA: 2 spec., 10.8, 13.4 mm, patch reef near Long Key Reef, Dry Tortugas, 1.5-2.5 m, 11-12 May 1979, FSBC I 32074. —3 spec., 10.9-14.7 mm, Long Key Reef, Dry Tortugas, intertidal, 11-12 May 1979, FSBC I 32075. —1 spec., 10.1 mm, Bird Key Reef, Dry Tortugas, 0.5-1.0 m, 4 Oct 1979, FSBC I 32079. —1 spec., 10.7 mm, Bird Key Harbor, Dry Tortugas, 2 m, 21 Aug 1981, FSBC I 32487. —4 spec., 6.1-10.6 mm, Garden Key, Dry Tortugas, 1-2 m, 13 May 1979, FSBC I 32076. —1 spec., 11.3 mm, Garden Key, 1-2 m, 5 Oct 1979, FSBC I 32080. —3 spec., 7.3-12.8 mm, Key West, CAS 063314. —1 spec., 9.5 mm, West Summerland Key, 0-1 m, 27 Sept 1981, FSBC I 32082. —1 spec., 5.4 mm, Missouri Key, 0.5-1.0 m, 25 July 1987, FSBC I 32491. —4 spec., 9.2-14.6 mm, north side Vaca Key, 1 Oct 1979, FSBC I 32077. —5 spec., 4.0-14.9 mm, northeast end Vaca Key, 0-1.5 m, 4 Aug 1980, FSBC I 32081. —1 spec., 9.2 mm, same location, 28 Sept 1981, FSBC I 32083. —5 spec., 7.2-11.1 mm, Bonefish Key, CAS 063313. —1 spec., 14.1 mm, north side Grassy Key, 0.5 m, 1 Oct 1979, FSBC I 32078. —2 spec., 5.0, 9.9 mm, east end Grassy Key, 0-1 m, 18 Mar 1968, FSBC I 6395. —4 spec., all curled, Burnt Point, Crawl Key, 2.5 m, July 1982, FSBC I 32488. —4 spec., all curled, same locality, 4 Aug 1982, FSBC I 32489. BAHAMAS: 1 spec., 13.2 mm, McLeanstown, east end Grand Bahama, 1-2 m, 24 May 1981, FSBC I 32486. —2 spec., 6.0, 13.0 mm, same locality, 27 Aug 1984, FSBC I 32084. —1 spec., curled, Georgetown, Great Exuma, 21 June 1974, FSBC I 32526. TURKS AND CAICOS ISLANDS: 1 spec., 13.6 mm, Providenciales, 0-2 m, 22 Sept 1986, FSBC I 32490. PUERTO RICO: 1 spec., 14.0 mm, 2 km east of La Parguera, 1 m, 17 Aug 1985, FSBC I 32085. —1 spec., 13.0 mm, Cayo Enrique, La Parguera, 1 m, 19 Aug 1985, FSBC I 32086.

DISTRIBUTION: Dry Tortugas and Florida Keys, Bahama Islands to Puerto Rico, Cuba, Jamaica, and the Cayman Islands, Aruba and Bonaire.

DESCRIPTION: Largest specimen 14.9 mm long, 8.9 mm wide including girdle; valves nearly entirely covered by smooth, black, brown, gray (rarely rose or yellow) girdle (Figs. 146, 147). Narrow, white longitudinal bars evident in jugal region.

Exposed parts (jugum) smooth, that of valve i semiovate, slightly wider than long; exposed jugal parts of



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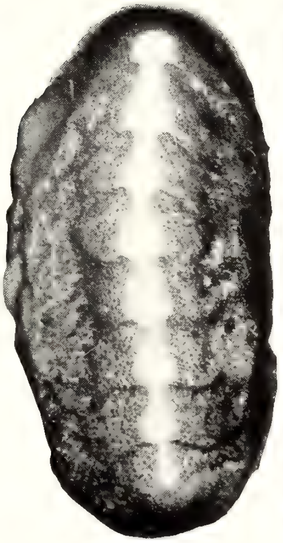

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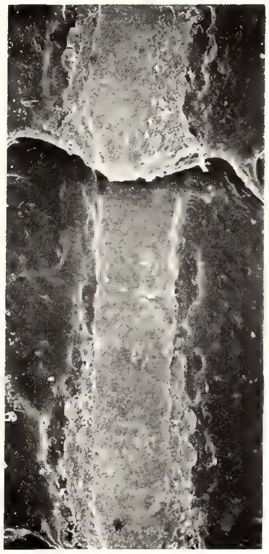

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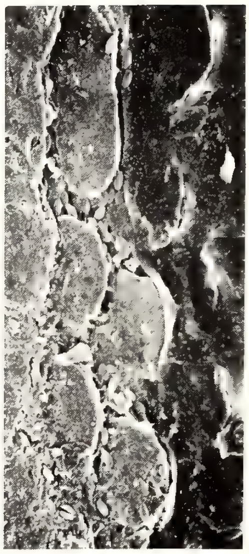

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Figs. 146-149. *Cryptoconchus floridanus* (Dall, 1889). **Fig. 146.** Whole specimen, 12.4 mm; Vaca Key, Monroe County, Florida; FSBC I 32081. **Fig. 147.** Whole specimen, 10.7 mm; same lot. **Fig. 148.** Jugum, valves iii-iv, same specimen as 147 (field width = 940 μm). **Fig. 149.** Rudimentary pustules bordering jugum; same specimen as 147 (field width = 175 μm).

valves ii-vii narrow, straight-sided for about 60% of length, thereafter expanded to truncate distal end, slightly elevated at central posterior beaks; valve viii narrow, straight-sided, with small, expanded, bulb-like terminus at low mucro. Tegmentum virtually absent on valves, only occasionally represented by few ovate, elongate pustules up to 80 μm long, 50 μm wide arranged parallel to jugal bars (Figs. 148, 149).

Girdle smooth, appearing granulose or warty under magnification; 18 anterior and sutural dorsal pores situated as in other Acanthochitonidae, bearing about 10 extremely slender, fine-tipped spicules up to 100 μm long; spicules at peripheral margin sparse, short (40 μm), with blunt tips; underside densely covered with short (70-80 μm), sharp-tipped spicules.

DISCUSSION: Pilsbry (1893) described the disarticulated valves of *Cryptoconchus floridanus* as white, pink or purple; the intermediate valves are rectangular, with a sinus before and behind; there are 5 anterior slits on valve i, single slits on the sides of valves ii-vii, and 2 posterior slits on valve viii. Specimens examined herein, when viewed through the fleshy underside, generally agreed with the standard 5-1-2 slit formula. However, the largest specimen (FSBC I 32081) has 6 unevenly spaced slits on valve i. Tegmental pustules have not been described for *C. floridanus*, but rudimentary pustules sometimes do occur on valves where the girdle does not extend flush with the margin of the jugum.

The Florida range of *Cryptoconchus floridanus* has not been extended since Dall's (1889b) original description of specimens from Cape Florida, Key Largo, Key West, and Dry Tortugas. The species occurs throughout the Bahama Islands and Greater Antilles, including Puerto Rico, Cuba (Jaume and Sarasúa, 1943), Jamaica (Humfrey, 1975), and the Cayman Islands (Abbott, 1958). In the southern Caribbean, *C. floridanus* has been reported from Aruba and Bonaire (Kaas, 1972). The species has not been reported in the western Caribbean from Mexico to Colombia.

DISCUSSION

More specimens must be examined before definitive conclusions can be made on the composition and relationships of the Acanthochitonidae of the Caribbean region. Of the 14 recognized species, only *Cryptoconchus floridanus* has not been involved in long-term or recent taxonomic confusion. Thus, nearly all published records must be considered questionable, and the specimens upon which those records were based must be re-examined. In addition, more collections of Acanthochitonidae need to be made in the Lesser Antilles and along the Caribbean coasts of Central and South America. I examined far more material from Florida and the northern Caribbean region than from the southern Caribbean. That imbalance also occurs in published literature and probably will be found in the unreported museum collections. To my knowledge, there is no published record of any polyplacophoran from the area between Roatan, Honduras, and Limon, Costa Rica, yet that area contains the vast, shallow Honduras-Nicaragua shelf which exceeds in size the Bahama Banks. Given those cautions, some observations on the Caribbean Sea Acanthochitonidae seem warranted.

Occurrence of species may be limited by distributional barriers, habitat availability, and environmental stress near the northern boundary of the Caribbean region. Only *Acanthochitona pygmaea* occurs at Bermuda. In fact, only six of approximately fifty known species of shallow-water Caribbean Polyplacophora occur at Bermuda (Jensen and Harasewych, 1986). The paucity of species at Bermuda probably is due to long-term climate fluctuations and geographic isolation.

Seven species of Acanthochitonidae (*Acanthochitona andersoni, A. balesae, A. hemphilli, A. pygmaea, A. roseojugum, A. zebra,* and *Cryptoconchus floridanus*) are known from Florida, and it is unlikely that many more will be found there. Most of the species are restricted to tropical environments of the Florida Keys and southeast coast and do not occur in the more temperate environments of northeast and west Florida. There are no endemic species. Previous Florida records of *A. astrigera* and *Choneplax lata* are known or suspected to be erroneous; I have collected both species at various Caribbean locations, but I know of no similar habitats where they could occur in Florida.

The northern Caribbean fauna, which extends from Grand Bahama Island to Puerto Rico, the Virgin Islands, and northern Netherlands Antilles (St. Eustatius and Saba Bank) in the east and to Belize and Roatan in the west, is quite diverse. Eleven species are known in that fauna, including all of the Florida species plus *Acanthochitona astrigera, A. lineata, A. worsfoldi,* and *Chonoplax lata.* All eleven species have been collected at Grand Bahama Island, and all except *A. worsfoldi* have been collected at other northern Caribbean sites. It is likely that intensive collecting will reveal similar species richness at other northern Caribbean locations.

Only *Acanthochitona andersoni, A. astrigera,* and *Choneplax lata* are known with certainty from the Lesser Antilles south of the northern Netherlands Antilles. However, Ferreira (1985) reported *A. rhodea* from Barbados, so it would appear that a species of the *A. hemphilli* complex occurs there, and Ferreira's Barbados records of *C. lata* seem to be *A. worsfoldi.*

The southern Netherlands Antilles (Aruba, Bonaire and Curaçao) fauna is known to contain *Acanthochitona andersoni, A. astrigera, A. balesae,* the curiously restricted *A. bonairensis, A. rhodea, A. zebra, Choneplax lata,* and *Cryptoconchus floridanus.* A total of eight species is indicated.

The fauna of southern Caribbean coastal areas is poorest known. Along the entire expanse from Limon, Costa Rica to Trinidad, I have seen only specimens of *Acanthochitona andersoni, A. balesae, A. rhodea, A. venezuelana,* and a single specimen of an unknown *Acanthochitona* species from Galeta Island, Panama.

There is little evident relationship between Brazilian species of Acanthochitonidae and those of the Caribbean fauna. Only three of the seven species of *Acanthochitona* reported from Brazil were described from the Caribbean region, and Brazilian records of each of those three species are questionable. Statements of the Brazilian occurrence of *A. spiculosa* originally derived from E. A. Smith's (1890) report of *A. astrigera* at Fernando Noronha, but Righi (1971) also reported *A. spiculosa* from off São Paulo in 25 m depth, far deeper than the intertidal and shallow subtidal habitat otherwise known for *A. astrigera.* A report of Brazilian specimens of *A. pygmaea* by Righi (1971) was accompanied only by illustrations of spicules and radula and was published when the identity of that species was poorly understood; verified specimens of *A. pygmaea* have been seen only from Saba Bank northward to Bermuda. Brazilian records of *A. hemphilli* are based on specimens reported from depths of 47-115 m (Righi, 1971), whereas verified specimens have been seen only from Honduras and Puerto Rico northward to Florida and from depths not greater than 18 m.

None of the four species of *Acanthochitona* originally described from Brazil has been encountered in the Caribbean fauna, and each has characters which distinguish it from any Caribbean species. *Acanthochitona brunoi* Righi, 1971, has a broad, strongly furrowed jugum bounded by only small lateral tegmental areas whose anterolateral margins are concave. The jugum of *A. ciroi* Righi, 1971, is very broad, occupying more than half the total width of intermediate valves, but is smooth, not furrowed, and valve i has fine, rib-like rows of pustules (among other pustules) radiating toward the slits from the posteromedial margin of the tegmentum. Pustules of the tegmentum of *A. minuta* (Leloup, 1980) continue fully formed over the entire jugum. The jugum of *A. terezae* Guerra Júnior, 1983, is similarly ill-defined and covered with pustules, but the most distinctive features of that species occur on valve viii, where the forward extension of the small, rudimentary sutural laminae is far exceeded by that of the broad, anterolaterally constricted tegmentum.

Several taxonomic groups are evident among the Caribbean and eastern Pacific Ocean species of *Acanthochitona.* Each group, or species complex, contains two Caribbean and one eastern Pacific species as indicated by morphological similarities. Closely related species complexes recognized here include *Acanthochitona hemphilli* and *A. rhodea* (Caribbean) and *A. ferreirai* (eastern Pacific); *A. pygmaea* and *A. venezuelana* (Caribbean) and *A. avicula* (eastern Pacific); and *A. astrigera* and *A. lineata* (Caribbean) and *A. hirudiniformis* (eastern Pacific). Watters (1981) proposed another species complex containing *Acanthochitona andersoni* and *A. balesae* (Caribbean) and *A. arragonites* (Carpenter, 1857) (eastern Pacific). I have no study material of *A. arragonites* and so cannot verify that relationship.

Relationships among the other Caribbean species of *Acanthochitona* are less evident. Valve morphology of *A. roseojugum* resembles that of species in the *A. hemphilli* complex, and valves of *A. worsfoldi* resemble those of species in the *A. astrigera* complex. However, girdle spicules of *A. roseojugum* and *A. worsfoldi* hardly resemble spicules of species in those complexes, so only remote relationships to those species are proposed. *A. bonairensis* most resembles the European *A. fascicularis* and does not much resemble any other New World species.

The curious, underhanging posterior insertion plate with two nearly vestigial slits, as well as the form, number, and color of girdle spicules, suggest a relationship between *Acanthochitona zebra* and *Choneplax lata.* However, their resemblance probably represents convergence rather than close phylogenetic relationship. Only single species of *Choneplax* and *Cryptoconchus*, both Caribbean, are known in the New World.

Distributional patterns of taxa in two of the *Acantho-*

chitona species complexes are known sufficiently to allow speculation on their evolutionary history. *A. rhodea* and *A. venezuelana* each occurs only along the southern Caribbean coast, and each has a very similar cognate (*A. ferreirai* and *A. avicula*) in the eastern Pacific region, as well as less similar but still closely related congeners (*A. hemphilli* and *A. pygmaea*) in the northern Caribbean. These distributional patterns suggest at least two isolation-speciation events. In the first event, *A. pygmaea* (and probably *A. hemphilli*) diverged from the still-connected southern Caribbean-Panamic stocks before or during the Pliocene, as evidenced by *A. pygmaea* valves in Tertiary deposits. The valve reported as *A. spiculosa* from the North Carolina Pliocene [Berry, 1940: 213, pl. 10 (not pl. 12), figs. 5, 6] is not of *A. pygmaea*. However, Dall (1903), who previously reported *A. pygmaea* as *A. spiculosa*, listed both *A. pygmaea* and *A. spiculosa* in the Pliocene Caloosahatchie beds of south Florida. The first isolation event left the ancestors of *A. pygmaea* (and probably *A. hemphilli*) in the northern Caloosahatchian fauna and left species resembling *A. avicula* and *A. rhodea* in the southern Gatunian fauna (*sensu* Petuch, 1982). The known southern distributional limits of *A. hemphilli* (Honduras) and *A. pygmaea* (Saba Bank) occur precisely where Petuch (1982) identified areas of abrupt faunal shift between the northern and southern Caribbean fauna. Emergence of the Isthmus of Panama in the late Pliocene provided the barrier which resulted in later speciation among the *avicula*-like and *rhodea*-like progenetors.

Speciation mechanisms in the *Acanthochitona astrigera-lineata-hirudiniformis* species complex are less evident. The Caribbean *A. lineata* and eastern Pacific *A. hirudiniformis* are most similar in valve morphology and thus seem to have diverged most recently. To date, *A. lineata* is known only from the northern Caribbean, whereas *A. astrigera* occurs in both the northern and southeastern Caribbean. Ferreira (1985) reported *A. astrigera* from Caribbean Panama, but he included three species (*A. astrigera, A. lineata,* and *A. zebra*) within his concept of *A. astrigera.* Re-examination of his Panama material might provide additional clues to the evolutionary history of this species complex.

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CHITONS (MOLLUSCA: POLYPLACOPHORA) FROM THE COASTS OF OMAN AND THE ARABIAN GULF

PIET KAAS
RIJKSMUSEUM VAN NATUURLIJKE HISTORIE, P. O. BOX 9517,
2300 RA LEIDEN, THE NETHERLANDS
AND
RICHARD A. VAN BELLE
KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN,
VAUTIERSTRAAT 29, 1040 BRUSSELS, BELGIUM

ABSTRACT

Twelve species of chitons are reported from the coasts of Oman and the Arabian Gulf. Misidentifications are corrected for five of the seven species previously reported from that area. New records for the region include *Lepidozona luzonica* (Sowerby, 1842), *Callistochiton adenensis* Smith, 1891, *Chiton fosteri* Bullock, 1972, *Tonicia (Lucilina) sueziensis* (Reeve, 1847), and *Onithochiton erythraeus* Thiele, 1910. Two new species, *Acanthochitona woodwardi sp. nov.*, and *Notoplax arabica sp. nov.*, are described.

The chiton fauna of the Arabian Gulf, the Gulf of Oman and the Oman coast of the Arabian Sea has not been investigated thoroughly. Melvill and Standen (1901, 1906), reporting upon the mollusks of the Persian Gulf, Gulf of Oman and Arabian Sea, did not mention any species of Polyplacophora. Biggs (1958) reported *Chiton lamyi* Dupuis, 1917 (= *C. peregrinus* Thiele, 1910) and *C. (Acanthopleura) haddoni* from the Arabian Gulf, the latter from Hormuz Island, Iran, at the entrance of the Gulf. Bosch and Bosch (1982: 145), reported a single species, *Acanthopleura haddoni* Winckworth, 1927 (= *A. vaillantii* de Rochebrune, 1882), a common rock-dweller in the Red Sea and on the coasts of the northern Indian Ocean (except in the Arabian Gulf, where it is uncommon). Those authors admitted that "there are several species of chitons to be found in Oman, but most are small and present problems in identification." Their specimens, collected principally at the island of Masirah in the Arabian Sea, were identified provisionally by Kathleen R. Smythe. Smythe (1982) enumerated eight species of chitons but, in glaring contrast to the fine color photographs of gastropod and bivalve shells, she illustrated the chitons with primitive line-drawings, by which none are recognizable. Apart from several misidentifications, Smythe should be credited for establishing the occurrence of several well known and easily recognizable species from the Arabian Gulf. Glayzer *et al.* (1984) listed five species of chitons from Kuwait, including four listed previously by Smythe. In the present study we establish the occurrence of twelve species of chitons in littoral waters of the western Arabian Gulf, the western Gulf of Oman, and the Oman coast of the Arabian Sea.

HABITAT

A. J. Woodward provided the following descriptions of the Qatar stations where he collected chitons, mostly by snorkelling or scuba-diving. Ras Abruk (Fig. 1: no. 9) is a sheltered bay on the end of a peninsula. The predominantly limestone cliffs are ca. 10 m high, with raised fossil beds and sandy beaches. Large boulders of limestone and aggregates occur in the extreme shallows due to rock falls from the cliffs. Fasht (= limestone and aggregate slabs with shells, pieces of coral, etc.) occurs close to the shoreline and out to 30-40 m in a broad broken band that is frequently exposed at low tide and rarely covered by more than 30 cm of water. Beyond the fasht band there is a small drop-off of mostly weed-covered rocks, to a depth of about 2 m. Further offshore the substratum is composed of fine sand for about 300 m, beyond which coral and rock occur at a depth of 3-5 m. Chitons were always found in the fasht band, where summer temperatures are extremely high (50+°C). Therefore, the water temperature is often 40+°C in the shallows. Salinity is similarly high (40+ ppt by estimate).

Fuwairat (also spelled Fuwairet) (Fig. 1: no. 10) is a coastal location with 30 m high limestone cliffs and small bays at Jebel Fuwairat, about 1 km north of the village. Pebbly, loose rocks, that occur at the extreme edge of the white sand

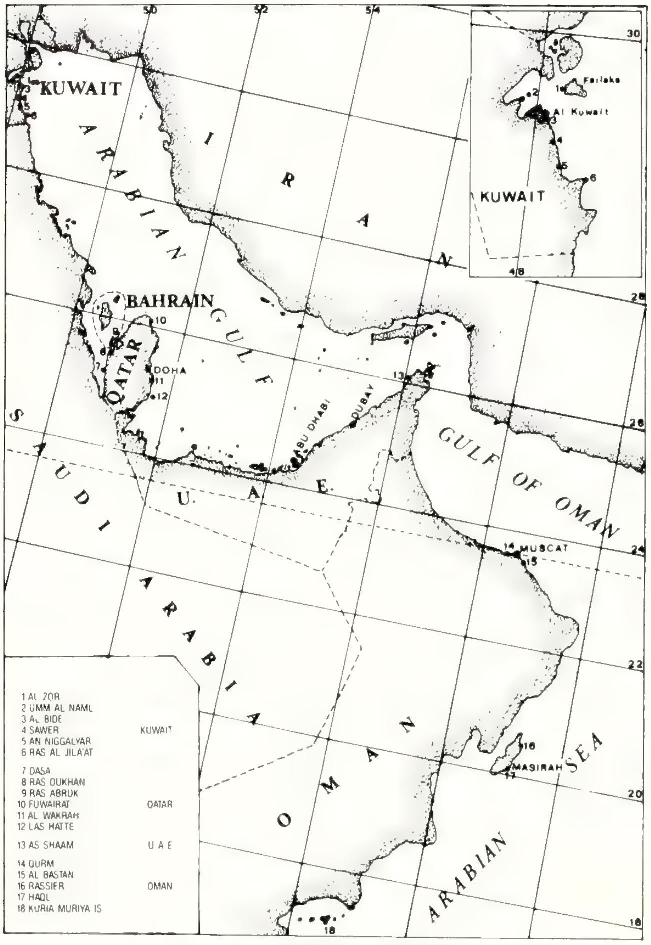


Fig. 1. Map of Oman and the Arabian Gulf.

beach, are frequently exposed at low tide (maximum tidal range ca. ± 1.5 m). A narrow band of clean sand about 20 m from shore can also be exposed during extreme low tides. Further offshore the substratum is composed of loose rock with some weed and algae cover, coral debris, small pieces of live coral and fine sand. Seaward, small patches of live coral occur on soft sand that becomes gravelly sand near coral heads. An extensive coral reef is located ca. 200 m from shore at a depth of 5 m. Chitons are found in the loose rock zone about 30-75 m from shore, usually on undersides of rocks or dead coral where the water depth rarely exceeds 1 m. Temperature is very high in the shallows, though in winter it drops below 11ºC. This gives an annual temperature differential of ca. 30ºC.

Wakrah is a small town south of Doha (Fig. 1: no. 11) with very wide sandy beaches backed by limestone ridges. In the extreme shallows near the beach broken fasht lies on top of shelly gravel and sand. Hard packed, fine, white, exposed sand bars are located about 50 m from the beach and extend to ca. 200-300 m from the shoreline. These are exposed at low tide. Following a slight drop-off into 1-1.5 m depths, there first occurs a band of fine white sand, then loose rock and dead coral covered by algae and weed. A second fine white sand area occurs beyond the first and is followed by another band of shell and coral debris and loose algae and weed covered rocks that rise to ca. 30 cm in height. Here chitons were occasionally found on the undersides of rocks. Chitons were also found on shells of *Pinna muricata* L. The chitons live on the parts of the shells which are deeply buried in the sand. Chitons were never found on the broken fasht. The temperature is high, ca. 2ºC less than that at Ras Abruk; the salinity is possibly higher.

Las Hatte (= Al Ashat), situated offshore from Umm Said (Fig. 1: no. 12), consists of a group of four small limestone islands with sandy beaches fringed by live coral about 75 m from shore where a fairly steep drop-off occurs. Chitons [= *Lepidozona luzonica* (Sowerby, 1842)] are found on dead valves of arkshells (Arcidae) from about 10 m down to the seabed at about 25-28 m. The substratum comprises a mixture of silty black mud and sponges. Salinity is ca. 40-50 ppt at the surface and increases with depth. The water temperature in summer is lower than at other locations, rarely exceeding 36ºC; temperature in winter is ca. 12-15ºC due to greater water depth.

The following abbreviations are used throughout the text: BG, Private collection of B. Glayzer; BMNH, British Museum (Natural History), London; FH, Private collection of F. Hinkle; KS, Private collection of K. Smythe; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN, Muséum National d'Histoire Naturelle, Paris; RMNH K, Private collection of P. Kaas, now in Rijksmuseum van Natuurlijke Historie, Leiden; VB, Private collection of R. Van Belle; ZMHU, Zoologisches Museum an der Humboldt Universität, Berlin.

SYSTEMATIC ACCOUNTS

Class Polyplacophora

Order Neoloricata

Suborder Ischnochitonina

Family Ischnochitonidae Dall, 1889

Subfamily Ischnochitoninae

Genus *Ischochiton* Gray, 1847

Type Species: *Chiton textilis* Gray, 1828 (by subsequent designation, Gray, 1847).

Subgenus *Ischnochiton s.s.*

Ischnochiton (I.) yerburyi (E. A. Smith, 1891)

Figs. 2-7

Chiton (Ischnochiton) yerburyi E. A. Smith, 1891: 420, pl. 33: fig. 6.

Ischnochiton yerburyi, Pilsbry, 1892: 101, pl. 20: fig. 11. Nierstrasz, 1905: 30. Thiele, 1910: 111, 113. Kaas, 1954: 5. Leloup, 1960: 35, fig. 5. Biggs, 1973: 374. Leloup, 1980: 10. Smythe, 1982: 83, fig. 17. Ferreira, 1983: 251, figs. 1, 2. Glayzer *et al.,* 1984: 324. Kaas, 1986: 11, figs. 8, 8a, b (synonymy).

(?) *Ischnochiton rufopunctatus* Odhner, 1919: 21, pl. 3: figs. 40, 41.

(?) *Ischnochiton (Radsiella) delagoaensis* Ashby, 1931: 40, pl. 6: figs. 63-66.

Ischnochiton haersoltei Kaas, 1954: 5, figs. 7-9.

Table 1. Distributional records of Polyplacophora in the Arabian Gulf and Oman. Species marked with an asterisk (*) also occur on the African coast of the Indian Ocean.

	Arabian Gulf				Oman	
Species	Kuwait	Bahrain	Qatar	U. A. E.	Gulf of Oman	Arabian Sea
**Ischnochiton yerburyi* Smith, 1891	+	+	+	−	+	+
I. winckworthi Leloup, 1936	+	−	+	+	−	−
Lepidozona luzonica (Sowerby, 1842)	−	+	+	+	−	−
Callistochiton adenensis Smith, 1891	−	−	−	−	−	+
Chiton peregrinus Thiele, 1910	+	−	+	+	+	+
**C. fosteri* Bullock, 1972	−	−	−	−	−	+
**C. (Rhyssoplax) affinis* Issel, 1869	+	−	+	−	+	−
**Acanthopleura vaillantii* de Rochebrune, 1882	−	(+)[1]	−	(+)[1]	(+)[1]	+
**Tonicia (Lucilina) sueziensis* (Reeve, 1847)	+	+	+	−	−	+
**Onithochiton erythraeus* Thiele, 1910	−	−	−	−	−	+
Acanthochitona woodwardi sp. nov.	+	−	+	−	−	−
Notoplax (Notoplax) arabica sp. nov.	+	−	+	−	−	−

[1] Reported by Biggs (1958: 271) from Hormuz Id., Iran, at entrance of Arabian Gulf. Collected by Smythe (in litt. 3 June 1987) on the Trucial coast of the Emirates, just inside the Gulf, at Khor Khaymal and Sharjah, and also at a point in Bahrain (!). Collected by Woodward at Dubai.

SYNTYPES: BMNH 1888.4.9.345.

MATERIAL EXAMINED. KUWAIT: 1 spec., 11.5 x 5.5. mm, Bide Circle, under stones in tidepool, F. Hinkle leg., 12 June 1978, FH; —1 spec., ca. 7 mm long, id., 20 Sept 1979, FH; —3 spec., max. 15 x 8 mm, id., 1 Aug 1981, FH; —2 spec., Kuwait Bay, on *Pinna muricata*, intertidal, 19 Sept 1975, B. Glayzer leg., BG 1427; —Numerous valves, Bahrain, in shell grit on beach, Nov 1971, F. van Nieulande don., VB 2667a. QATAR: 1 spec., 9 x 5 mm, Ras Abruk, under broken slabs of fasht, intertidal, May 1982, A. Woodward leg., KS; —6 spec., max. 10.5 x 5.5 mm, Fuwairat, on rocks and dead coral, 0-1 m, June 1985, A. Woodward leg., 4/KS, 2/RMNH K5105 (one disarticulated). OMAN: 3 spec., Gulf of Oman, Qurm, K. Smythe leg., 1979, KS; —2 spec., Arabian Sea, Masirah Id., Rassier, KS; —3 spec., Haql, K. Smythe leg., KS.

TYPE LOCALITY: Aden.

DISTRIBUTION: Indo-Arabian coasts from Karachi, Pakistan, to Aden in Yemen, and in the Red Sea to the Gulf of Aqaba, Israël; African coast from Somalia to Zanzibar (many of these records are unconfirmed).

DESCRIPTION: This taxon was adequately described and illustrated by E. A. Smith (1891: 420, pl. 33 fig. 6) except for details of girdle armature and radula which follow (see also Figs. 2-5). Dorsal girdle scales (Fig. 6) broadly rounded, moderately curved, ca. 100 x 80 μm, with 12-15 elevated, slightly converging riblets separated by somewhat narrower, rather deep grooves.

Central tooth of radula (Fig. 7) narrow, abruptly widening distally to umbrella-like blade; first lateral teeth as long as central tooth, narrow, with inwardly curved, roundish blade; major lateral teeth with bidentate head, inner cusp much stronger than outer one, shaft with a short, trunk-like appendix just under and before head; spatulate uncinal with bluntly pointed, outwardly incised cusp.

DISCUSSION: Ferreira (1983: 251) combined all Indian Ocean species of *Ischnochiton* with "reticulate, thimble-like sculpture." Whether he was correct in synonymizing *Ischnochiton sansibarensis* Thiele, 1910, *I. delagoaensis* Ashby, 1931, *I. kilburni* Kaas, 1979, from Mozambique, and *I. rufopunctatus* Odhner, 1919, from Madagascar, with *I. yerburyi* cannot be decided here. Close reexamination of the types could reveal a complex of sibling species, rather than one variable species. As far as we can ascertain, *I. haersoltei* Kaas, 1954, from Manora Island, Karachi, does not differ from Gulf specimens of *I. yerburyi.*

Ischnochiton (I.) winckworthi Leloup, 1936

Figs. 8-15

Ischnochiton winckworthi Leloup, 1936: 51, figs. 1-9, 1949: 1, figs. 1, 2, 3A, 4-7, pl. 1; 1952: 15. Rajagopal and Subba Rao, 1974: 404, 409. Smythe, 1982: 83, fig. 16.
Ischnochiton ranjhai Kaas, 1954: 8, figs. 10-14.

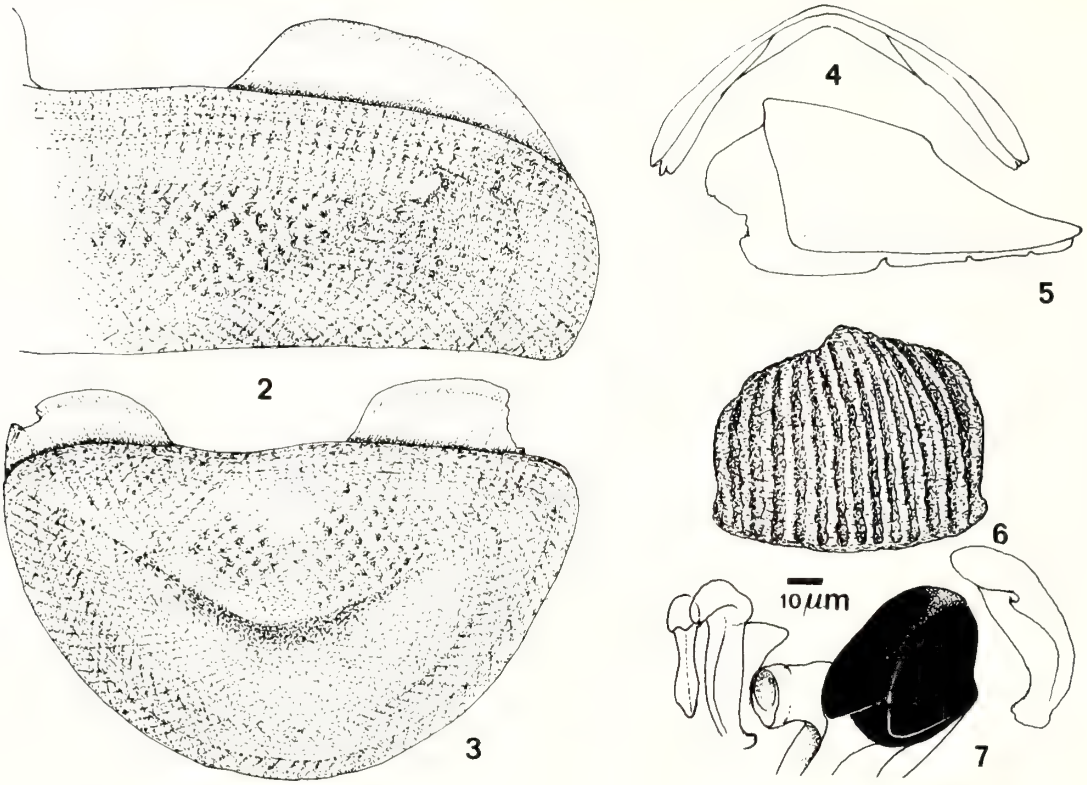
SYNTYPES: BMNH.

MATERIAL EXAMINED: KUWAIT: 1 spec., 7.5 x 4 mm, Bide Circle, under stones in tidepool, F. Hinkle leg., 20 Sept 1979, FH; —2 spec., max. 5 x 3.5 mm, id., 1 Aug 1981, FH; —2 spec., max. 7 x 4 mm, id., 10 Sept 1983, FH; —1 valve + girdle, Sawer, 1974, K. Smythe leg., KS; —1 spec., Kuwait Bay, 14 Feb 1975, B. Glayzer leg., KS. QATAR: 2 spec., Ras Dukhan, 15 Apr 1978, K. Smythe leg., KS. —9 spec., max. 10 x 5.5 mm, Ras Abruk, under broken slabs of fasht, intertidal, May 1982, A. Woodward leg., 7/KS, 2/RMNH K5097. —2 spec., Ras Abruk, 2-3 Nov 1978, A. Partridge leg., KS. —3 spec., max. 10 x 5.5 mm, Fuwairat, on rocks and dead coral, 0-1 m, June 1985, A. Woodward leg., KS. U. A. E.: 2 spec., 3.2 and 2.6 mm long, Abu Dhabi, K. Smythe leg., KS.

TYPE LOCALITY: Sri Lanka, near Trincomali, Dutch Bay.

DISTRIBUTION: Locally common along the shores of Malaysia, Andaman Islands, Burma, Sri Lanka, Pakistan, Kuwait, Qatar, U. A. E.; intertidal.

DESCRIPTION: Animals small, ca. 10 mm long, width ca. 2/3 length, largest specimen recorded 15 x 9.5 mm (Leloup, 1936: 51), oval, moderately raised (dorsal elevation 0.35-0.41), carinated, side slopes straight to slightly convex, valves not beaked. Color of tegmentum variable, beige, olivaceous, dark



Figs. 2-7. *Ischnochiton yerburyi* Smith (specimens from Fuwairat, Qatar, Apr 1985, A. Woodward leg. in coll. Smythe, RMNH K5105). **Fig. 2.** Valve IV, dorsal view, 3.7 mm wide. **Fig. 3.** Valve VIII, dorsal view, 3.7 mm wide. **Fig. 4.** Camera lucida sketch of valve IV, rostral view, 5.5 mm wide. **Fig. 5.** Lateral view of valve VIII, 2.4 mm wide. **Fig. 6.** Dorsal girdle scale. **Fig. 7.** Central, first lateral, major lateral and spatulate uncinal radula teeth.

greyish green, with roughly symmetrical blotches of dirty white on central part of valves. Many specimens with 2-3 dark spots at posterior margin of valves, some specimens uniformly roseate, more exceptionally, white or brownish.

Head valve (Fig. 8) semicircular, front slope straight, posterior margin widely V-shaped, weakly notched medially. Intermediate valves (Figs. 9, 10, 13) broadly rectangular, front and hind margins nearly straight, parallel-sided, apices hardly or not indicated, side margins rounded, lateral areas little raised but neatly marked. Tail valve (Figs. 11, 12) somewhat less than semicircular, mucro not prominent, slightly anterior, posterior slope concave.

Tegmentum granulose, sculpture often obsolete in younger specimens, variable in older ones. In most commonly occurring form, head valve of adult specimen sculptured with 36-40 radiating, somewhat irregular, granulose riblets, becoming obsolete toward apex, growth lines hardly or not indicated, lateral areas of intermediate valves with 4-5 similar radiating riblets, some bifurcating near outer margin, central areas, and antemucronal area of tail valve, with weak, fine, longitudinal riblets, 10-15 per side, becoming obsolete toward the finely quincuncially granulose jugal area, postmucronal area of tail valve sculptured like head valve.

Articulamentum whitish to light roseate, tegmental color visible, apophyses thin, sharp, moderately wide, evenly arched, jugal sinus straight, ca. 1/5 width of valve, insertion plates short, slit formula 8-11/ 1/ 9-10, slit rays finely indicated, teeth sharp, smooth, eaves solid.

Girdle moderately wide with alternating bands of yellowish and greyish green, dorsally covered with strongly bent, imbricating scales, ca. 150 x 120 µm; top rounded, ornamented with ca. 10 strong ribs wider than interstices (Fig. 14). Margin with fringe of short, white, torpedo-shaped spicules. Ventral side of girdle paved with radiating rows of elongate rectangular, smooth scales, 67 x 20 µm. Radula (Fig. 15) with narrow central tooth bearing a roundish, upwardly curled blade; first laterals equally narrow, ending in inwardly curved, hook-shaped blade; major laterals with strong, sharply pointed main cusp and short minor denticle on outside. Gills holobranchial, abanal, 18 ctenidia per side in 7.4 mm specimen.

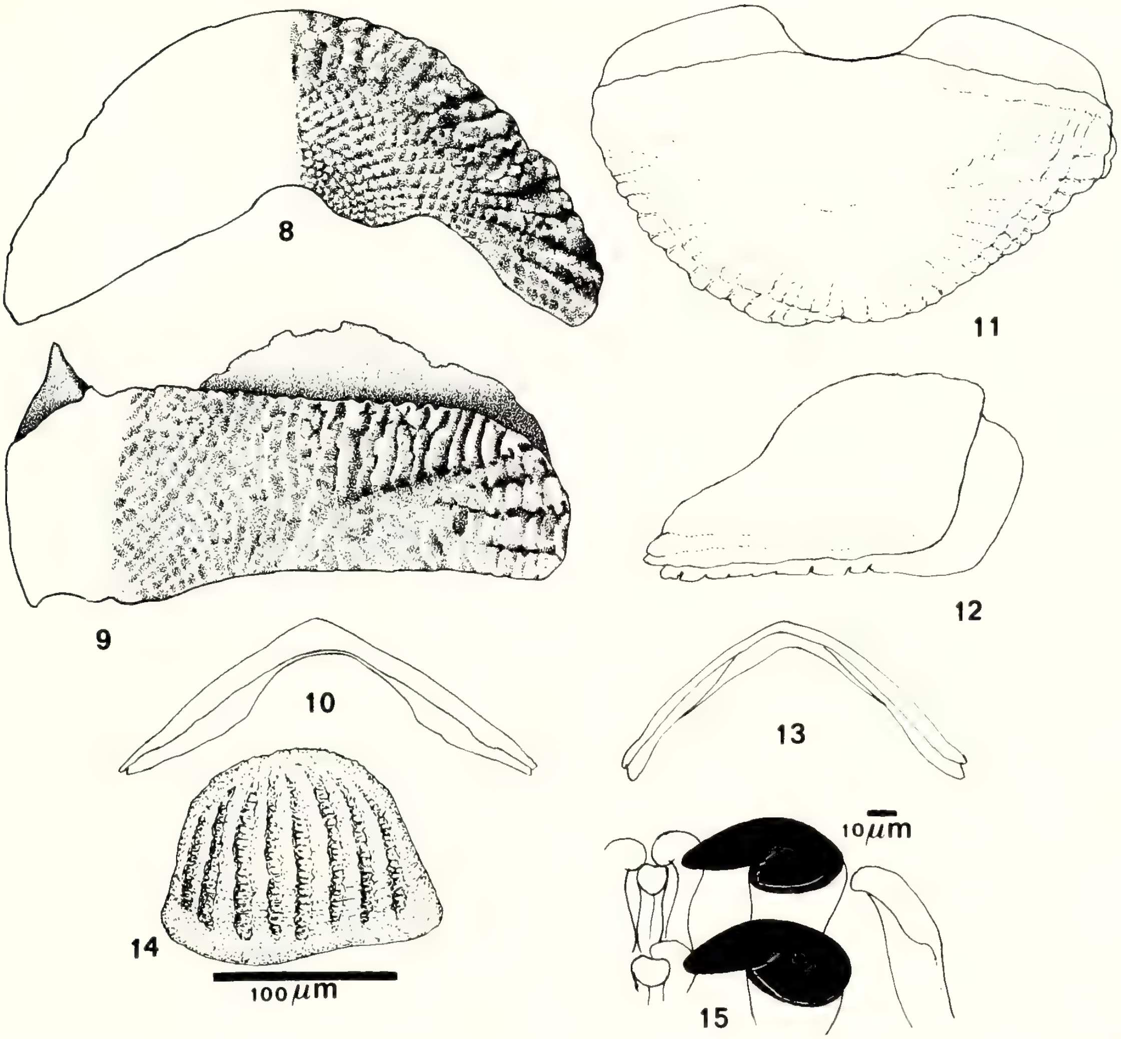
Genus *Lepidozona* Pilsbry, 1892

Type Species: *Chiton mertensii* von Middendorff, 1847 (by original designation).

Subgenus *Lepidozona* s.s.
Lepidozona (L.) luzonica (Sowerby, 1842)

Figs. 16-23

Chiton luzonicus Sowerby, 1842: 104. Reeve, 1847: pl. 25: sp. and fig. 167. Van Belle, 1982: 473.



Figs. 8-15. *Ischnochiton winckworthi* Leloup [Figs. 8-10: paratype of *Ischnochiton ranjhai* Kaas, 1954 (H. Heyn, del.), RMNH K3422; Figs. 11-15, specimen from Ras Abruk, Qatar, May 1982, A. Woodward leg. in coll. Smythe, RMNH K5097]. **Fig. 8.** Valve I, dorsal view, 3.7 mm wide. **Fig. 9.** Valve III, dorsal view, 3.5 mm wide. **Fig. 10.** Camera lucida sketch of valve VIII, rostral view, 3.8 mm wide. **Fig. 11.** Dorsal view of valve VIII, 4.7 mm wide. **Fig. 12.** Lateral view of valve VIII, 2.7 mm wide. **Fig. 13.** Rostral view of valve IV, 5.3 mm wide. **Fig. 14.** Dorsal girdle scale. **Fig. 15.** Central, first lateral, major lateral and spatulate uncinal girdle teeth.

Ischnochiton (Lepidozona) luzonicus Pilsbry, 1893: pl. 38, figs. 31-32; 1894: 85.

Ischnochiton luzonicus Nierstrasz, 1905: 34. Hidalgo, 1905: 271; Faustino, 1928: 123.

Callistochiton finschi Thiele, 1910: 86, pl. 8: figs. 57-60; 1911: 402. Ashby, 1923: 236. Iredale and Hull, 1925: 354. Ferreira, 1974: 163; 1978: 39.

Solivaga finschi Iredale and Hull, 1925: 355, pl. 40: figs. 14-16. Cotton, 1964: 55.

Lorica (Solivaga) finschi Thiele, 1929: 18.

Lepidozona luzonica Kaas and Van Belle, 1987: 245, fig. 111, map 52.

non *Ischnochiton (Lepidozona) luzonicus* Ang, 1967: 401, pl. 5: figs. 1-5 (= *Chiton* sp.).

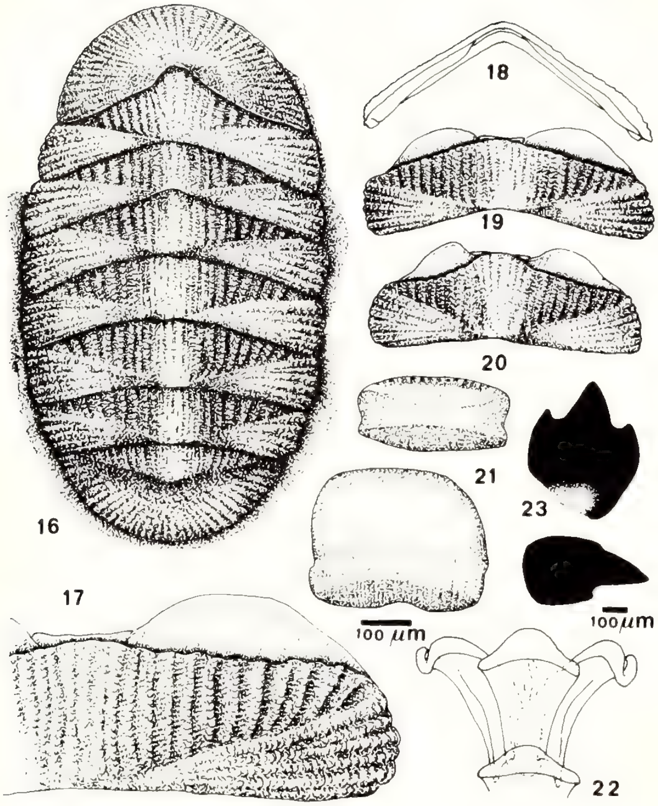
LECTOTYPE: BMNH 1979. 175/1 (by subsequent designation, Kaas and Van Belle, 1987).

MATERIAL EXAMINED: BAHRAIN: 1 valve, in shell grit on beach, Nov. 1971, F. van Nieulande don., VB 2975a. QATAR: 2 spec., Fuwairat, June 1985, A. Woodward leg., 1/KS 1/RMNH K5100. —4 spec., Las Hatte, on dead shells, 10-20 m, 26 July 1985, A. Woodward leg., 2/KS, 1/RMNH K5099, 1/VB 2975b (disarticulated); —7 valves (mounted on slide) Fuwairat or Las Hatte, June/July 1985, A. Woodward leg., KS. U. A. E.: 1 spec. (in alcohol), Abu Dhabi, K. Smythe leg., 4.2 mm long, KS.

TYPE LOCALITY: Philippines, province Albay, Isle of Luzon, Sorsogon, 27 m.

DISTRIBUTION: Eastern coast of Sumatra (Java Sea), Singapore (as *Callistochiton finschi*), Bahrain, Qatar and U. A. E.

DESCRIPTION: Animal small, lectotype (Fig. 16) 9.2 x 5.8 mm, largest specimen 12 x 7 mm (Iredale and Hull, 1925: 355, as *Solivaga finschi*), oval, moderately elevated (dorsal elevation



Figs. 16-23. *Lepidozona luzonica* (Sowerby) [Fig. 16, lectotype: Figs. 17-23, paralectotypes (BMNH 1979.175)]. **Fig. 16.** Whole specimen, dorsal view, 5.8 mm wide. **Fig. 17.** Right half of valve III, dorsal view, 4.6 mm wide. **Fig. 18.** Camera lucida sketch of valve III, rostral view, 7.3 mm wide. **Fig. 19.** Valve III, dorsal view, 7.3 mm wide. **Fig. 20.** Valve II, dorsal view, 6.9 mm wide. **Fig. 21.** Dorsal girdle scales. **Fig. 22.** Central and first lateral radula teeth. **Fig. 23.** Heads of major lateral teeth.

0.36-0.39) carinated, side slopes straight, valves not beaked. Color of tegmentum yellowish to greenish with, on central areas, few longitudinal streaks of darker tone, or buff, sparsely spotted with bluish green.

Head valve semicircular, front slope somewhat concave, hind margin widely V-shaped, deeply notched in middle, tegmentum sculptured with low, radial, often bifurcating, granulose riblets, 40-50 in number along outer margin, becoming obsolete toward apex. Intermediate valves (Figs. 17-20) broadly rectangular, front and hind margins straight, parallel-sided, side margins rounded, apices inconspicuous, lateral areas little raised, 5-6 riblets, up to 7-9 by splitting, central areas with 12-16 longitudinal, granulose ridges per side, ridges close-set and little pronounced on jugal areas, gradually more widely spaced and elevated toward side margins, interspaces finely, densely, but irregularly, transversely grooved. Tail valve subsemicircular, almost as wide as head valve, mucro at anterior third of valve, not prominent, postmucronal area rather flat, sculptured like head valve, ca. 32 riblets along outer margin, antemucronal area sculptured like central areas.

Articulamentum glossy white, apophyses very wide, short, rounded, connected across shallow sinus by short, slightly concave, laminated jugal plate, weakly notched at sides, slit formula 11-14/ 1/ 10-13, slits inequidistant, slit rays indicated, teeth short, weakly grooved on outside, eaves narrow, solid.

Girdle buff-colored, sometimes banded with bluish green, dorsally covered with obliquely implanted, slightly bent, more or less rectangular scales, with 12-16 obsolete ribs, up to 125 µm long, 188 µm wide in mid-girdle, smaller toward the outer margin (Fig. 21).

Central tooth of radula (Fig. 22) narrow at base, gradually widening to strong, rounded blade, first lateral tooth about as long as central one, slender, with somewhat distorted blade, major lateral (Fig. 23) with a tricuspid head, denticles sharply pointed, central one longer than others.

DISCUSSION: The present specimens undoubtedly are conspecific with *Lepidozona luzonica*, differing only in a less pronounced sculpture; radula and girdle armature are exactly like specimens of *L. luzonica* from elsewhere. Specimens from the Arabian Gulf extend the known range of *L. luzonica* considerably to the west and establish the presence of *Lepidozona* in the northwestern Indian Ocean.

Subfamily Callistoplacinae Pilsbry, 1893

Genus *Callistochiton* Carpenter in MS; Dall, 1879

Type Species: *Callistochiton palmulatus* Carpenter in MS (by monotypy, Dall, 1879).

Callistochiton adenensis (E. A. Smith, 1891)

Figs. 24-27

Chiton (Callistochiton) adenensis E. A. Smith, 1891: 421, pl. 33: fig. 7.

Callistochiton adenensis Pilsbry, 1893: 276, pl. 59: fig. 45. Nierstrasz, 1905: 41. Sykes, 1907: 31. Thiele, 1910: 84, pl. 8: figs. 49-51. Ashby, 1923: 233. Leloup, 1952: 30; 1953: 1, fig. 1. Kaas, 1979: 861. Ferreira, 1979: 463. Zeidler and Gowlett, 1986: 114.

Lepidopleurus rochebruni Jousseaume, 1893: 102. Nierstrasz, 1905: 10; 1906: 145, 157.

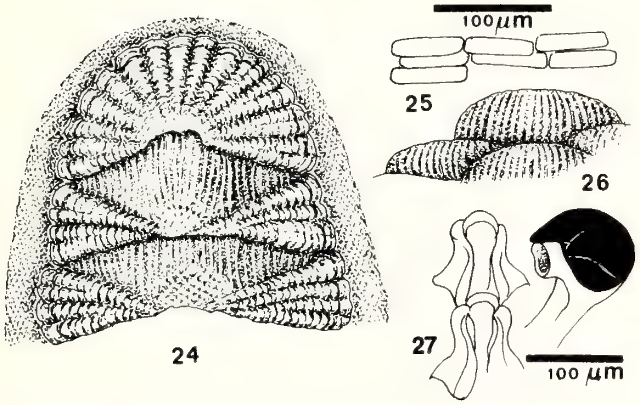
HOLOTYPE: BMNH.

MATERIAL EXAMINED: OMAN: 2 spec., max. 24 x 12 mm, Al Bastan or Masirah Id., Mar 1984, D. Bosch leg., 1/KS, 1/RMNH K5101. —1 spec., 16 mm (curled), Arabian Sea, Masirah Id., I. 1984, D. Bosch leg., KS; —1 spec., id., between Haql and Rassier, K. Smythe leg., KS. —1 spec., 18 mm, Rassier, K. Smythe leg., KS. —2 spec., 18.5. 18 mm long, (disarticulated), Rassier, 9 Feb 1982, K. Smythe leg., 1/KS, 1/VB 2976a.

TYPE LOCALITY: Aden.

DISTRIBUTION: Gulf of Aden; Arabian coast of Oman; possibly Gulf of Oman.

DESCRIPTION: Girdle densely covered with strongly imbricating, wide, short, oval, curved scales, with more than twenty elevated riblets, narrow, latticed interstices, ca. 140 x 50 µm; marginal scales small and narrow, bluntly conical, 25 x 50 µm, with ca. 6 ribs; ventral side of girdle covered with transverse rows of rectangular scales, ca. 60 x 15 µm (Figs. 24-26).



Figs. 24-27. *Callistochiton adenensis* (Smith) (specimen from Oman, Masirah Id. or Al Bastan, Mar 1984, D. Bosch leg. in coll. Smythe, RMNH K5101). **Fig. 24.** Valves 1-3 in situ, 12 mm wide. **Fig. 25.** Ventral girdle scales. **Fig. 26.** Dorsal girdle scales. **Fig. 27.** Central, first lateral and major lateral radula teeth.

Central tooth of radula (Fig. 27) somewhat pinched in middle, with semi-oval, rather narrow blade; first laterals somewhat S-shaped, embracing central tooth, with broad exterior wing in basal part and small rounded blade; major laterals with bicuspid head, denticles stout, sharply pointed, interior one slightly longer, shaft with short, curved appendix at inside of head; spatulate uncinals with narrow, rounded cutting edge.

Short, poorly illustrated original description of this species was amplified by Thiele (1910) who produced good figures of the valves, and by Leloup (1953), who also figured the girdle elements.

Family Chitonidae Rafinesque, 1815

Subfamily Chitoninae

Genus *Chiton* Linnaeus, 1758

Type Species: *Chiton tuberculatus* Linnaeus, 1758 (by subsequent designation, Dall, 1879).

Subgenus *Chiton s.s.*

Chiton (C.) peregrinus Thiele, 1910

Figs. 28-30

Chiton (Clathropleura) peregrinus Thiele, 1910: 90, pl. 9: figs. 23-27.
Chiton lamyi Dupuis, 1917: 538. Biggs, 1958: 271. Smythe, 1982: 82, fig. 15. Glayzer *et al.*, 1984: 324.
Chiton lamyi var. *reticulatus* Dupuis, 1918: 532.
Chiton wallacei Winckworth, 1927: 206, pl. 29: figs. 5-8.
Chiton iatricus Winckworth, 1930: 78, pl. 8b. Smythe, 1982: 82.
Chiton iatricus var. *winckworthi* Kaas, 1954: 2.
Chiton peregrinus Bullock, 1972: 238, pl. 44: figs. 1, 2, 10 (bibliography and synonymy). Ferreira, 1983: 268. Zeidler and Gowlett, 1986: 113.

SYNTYPES: ZMHU.

MATERIAL EXAMINED: KUWAIT: 4 juv. spec., Falaika Id., Al Zor, on rocks, intertidal zone, 10 Nov 1975, B. Glayzer leg., BG 1428 (as *Chiton lamyi*). QATAR: 3 spec., Dasa, K. Smythe leg., KS. U. A. E.: —1 partly disarticulated spec., As Shaam, K. Smythe leg., KS. OMAN: 6 spec., max. 37 x 22 mm, Al Bastan or Masirah Id., Mar 1984, D. Bosch leg., KS. —3 spec., Gulf of Oman: Qurm, 1979, K. Smythe leg., KS. —2 spec., max. 30 x 17 mm, Muscat, Mar 1969, D. Bosch leg., VB 2651a. —2 spec. + partly disarticulated + 1 disarticulated red spec. + 6 valves, Arabian Sea, Masirah Id., 12 Jan 1984, D. Bosch leg., KS. —3 spec. + 8 valves, id., Rassier, K. Smythe leg., KS. —23 spec., max. 28 x 20 mm (slightly curled), between Rassier and Haql, K. Smythe leg., KS. —3 spec., Haql, K. Smythe leg., KS.

TYPE LOCALITY: S Africa, ? Algoa Bay (in error = Aden, *fide* Bullock, 1972).

DISTRIBUTION: Widely distributed in the northwestern Indian Ocean from the north coast of western India to the Arabian Gulf and westward to the entrance of the Red Sea; intertidal in rocky areas.

DESCRIPTION: Specimens large, up to 7 cm long, greater than 4 cm wide. Shells, older animals, typically strongly eroded; young specimens with two thread-like radial riblets on lateral areas, one accompanying diagonal mark, another at short distance from posterior margin (Fig. 28). Tegmentum always granulate, granules on central areas arranged in somewhat wavy series perpendicular to diagonal lines, converging toward jugum. Color mostly greyish green, sometimes with black markings, valves of disarticulated specimen (Masirah Id., Oman) reddish all over along with articulamentum.

Girdle paved with strong, large, imbricating scales, with lozenge-shaped base, strongly bent, smooth on outside if not eroded (Fig. 29); scales ca. 0.75 mm wide, slightly less high, bluntly pointed at top. Central tooth of radula very narrow, sagittate, first laterals broad at base, narrowing distally, without blade; major laterals with simple, oval head without cusp (Fig. 30).

DISCUSSION: This species was well described by several authors who, owing to intraspecific variation and state of preservation, created different names for it. The complicated synonymy was clearly established by Bullock (1972). It is by far the most common chiton on the Indo-Arabian coasts.

Chiton (C.) fosteri Bullock, 1972

Figs. 31-33

Chiton fosteri Bullock, 1972: 245, pl. 44: figs. 6-9. Kaas, 1979: 862.

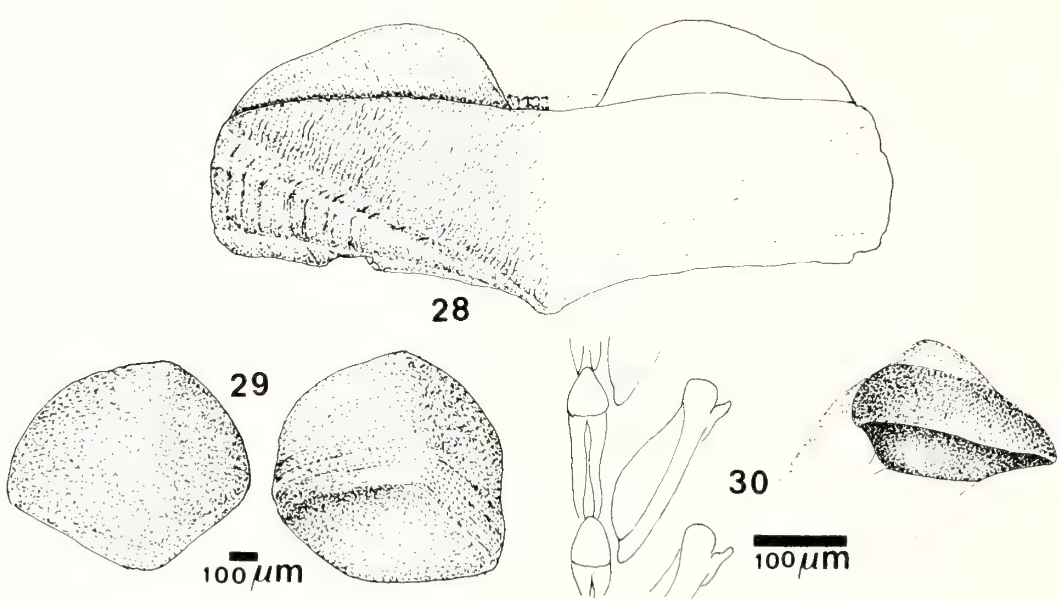
HOLOTYPE: MCZ 279166.

MATERIAL EXAMINED: OMAN: 1 spec., 40.5 x 21 mm, Arabian Sea, Masirah Id., Haql, K. Smythe leg., KS.

TYPE LOCALITY: Madagascar, Ile Ste Marie, Ankoalamare.

DISTRIBUTION: Madagascar, Mozambique, the Comoro Archipelago, Zanzibar and Kenya; locally common.

DESCRIPTION: Single specimen bluish green with faint zebra-pattern of brownish concentric lines (Fig. 31). Slit formula 9/1/16.



Figs. 28-30. *Chiton peregrinus* Thiele (Fig. 28: specimen from Manora Id., Karachi, Pakistan, 15 Feb 1953, S. M. H. Bilgrani leg., RMNH K4705; Figs. 29-30: specimen from Oman, Masirah Id., between Haql and Rassier, K. Smythe coll.). **Fig. 28.** Valve V, dorsal view, 8.9 mm wide. **Fig. 29.** Dorsal girdle scales, left dorsal, right ventral view. **Fig. 30.** Central, first lateral and major lateral radula teeth.

Dorsal girdle scales (Fig. 32) spindle-shaped, base elongate, lozenge-shaped, dorsal surface strongly convex, apparently smooth. Under high magnification scales appear finely punctate-lineate toward base, minutely bubbled around top. Scales on mid-girdle measure ca. 680 x 300 μm. Radula (Fig. 33) central tooth almost linear, with narrow, sagittal blade; major laterals closely packed, with oval head, edge of free margin sharp.

DISCUSSION: This species was well described by Bullock (1972). Additional observations were added by Kaas (1979).

Subgenus *Rhyssoplax* Thiele, 1893

Type Species: *Chiton janeirensis* Gray, 1828, *sensu* Thiele, 1893 (= *Chiton affinis* Issel, 1869) (by subsequent designation, I.C.Z.N., 1971).

Chiton (Rhyssoplax) affinis Issel, 1869

Figs. 34-40

Chiton affinis Issel, 1869: 234. Beu *et al.*, 1969: 184. Yaron, 1973: 15. Sabelli, 1974: 75. Fischer, 1978: 43.

Lepidopleurus bottae de Rochebrune, 1882: 192. Ferreira, 1983: 270, fig. 24.

Callistochiton heterodon savignyi Pilsbry, 1893: 277, pl. 60: fig. 16. Ferreira, 1983: 270.

Chiton olivaceus var. *affinis*, Leloup, 1952: 27, fig. 11, pl. 4: fig. 4. (bibliography and synonymy); 1960: 36. Sabelli and Spada, 1970: 6.

Callistochiton barnardi, Smythe, 1982: 81, fig. 14 (*non* Ashby, 1931). Glayzer *et al.*, 1984: 324.

Rhyssoplax affinis, Ferreira, 1983: 268, fig. 22.

LECTOTYPE: MNHN (by subsequent designation, Ferreira, 1983).

MATERIAL EXAMINED: KUWAIT: 2 spec., max. 12 x 6 mm, Bide Circle, under stones in tidepool, F. Hinkle leg., 20 Sept 1979, FH; —3 spec., max. 11.5 x 5 mm, id., 1 Aug 1981, FH; —2 spec., max. 10 x 5.5. mm, id., 10 Apr 1983, FH; —6 spec. (as *Callistochiton barnardi*), Kuwait Bay, on underside of rocks, intertidal zone, 19 Sept 1975, B. Glayzer leg., 5/BG 1426, 1/KS (disarticulated). QATAR: 10 spec., max. 15 x 8 mm, Ras Abruk, under broken slabs of fasht, intertidal, May 1982, A. Woodward leg., 6/KS, 2/RMNH K5104, 2/VB 2768b; —4 spec. (one heavily damaged), Ras Abruk, 3 Nov 1978, A. Partridge leg., KS. —13 spec., max. 14 x 6.5 mm, Fuwairat, on rocks and dead coral, 0-1 m, June 1985, A. Woodward leg., 12/KS, 1/RMNH K5103; .2 spec., Al Wakrah, K. Smythe leg., KS. OMAN: 2 spec., Gulf of Oman, Qurm, 1979, K. Smythe leg., KS.

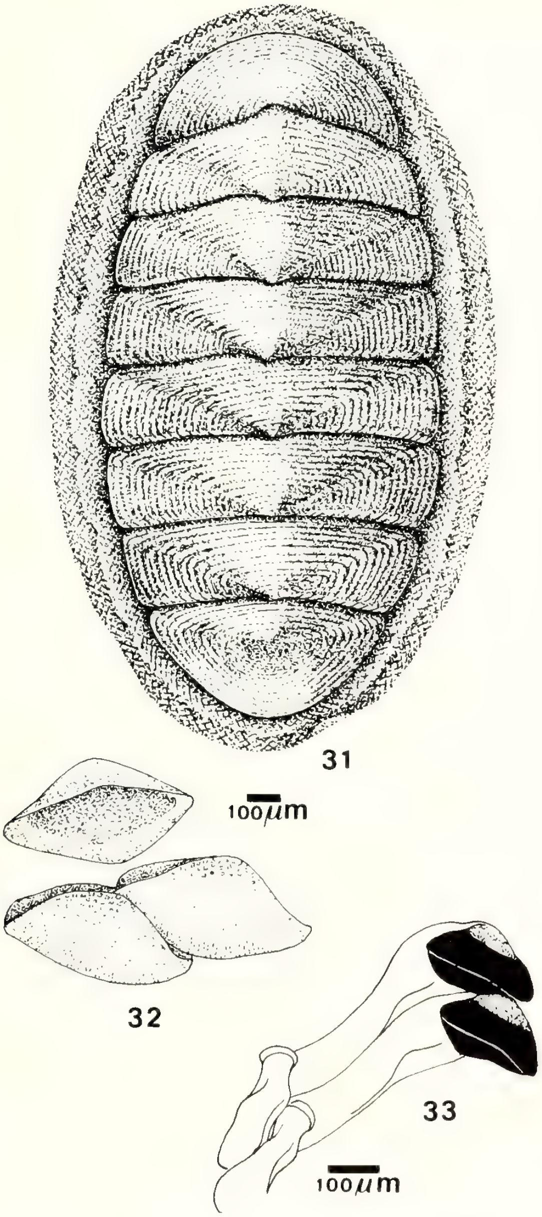
TYPE LOCALITY: Gulf of Suez.

DISTRIBUTION: Gulf of Suez, Red Sea and Somalia (southernmost record Sar Uanle), Arabian Gulf, the Gulf of Oman; intertidal to shallow subtidal.

DESCRIPTION: Dorsal girdle scales regularly imbricating, implanted in cuticula of girdle by diamond-shaped base, strongly curved dorsally, round-topped, ornamented with ca. 8 broad flat, weakly convergent ribs separated by narrow grooves, ca. 285 x 140 μm (Figs. 34-39).

Radula (Fig. 40) with narrow central tooth, blade narrowly U-shaped; first laterals broad at base, in middle with wing-like procession on inner sides, abruptly narrowing distally, ending bluntly rounded without blade; major laterals with broad, oval head, free margin sharply edged; on the inside of it the shaft bears a slender, trunk-like appendix.

DISCUSSION: The quite extensive original description (Issel, 1869) has been supplemented by several authors. Leloup (1952) produced detailed figures of the girdle elements. Yaron (1973) demonstrated the consistent morphological differences



Figs. 31-33. *Chiton fosteri* Bullock (specimen from Oman, Masirah Id., Haql, K. Smythe leg. and coll.). **Fig. 31.** Whole specimen, dorsal view, 27.6 mm wide. **Fig. 32.** Dorsal girdle scales, above ventral view, below dorsal view. **Fig. 33.** First and major radula teeth.

between *Chiton affinis* and the related Mediterranean Sea species *C. (R.) olivaceus* Spengler, 1797. Ferreira (1983) described the radula.

Subfamily Acanthopleurinae Dall, 1889

Genus *Acanthopleura* Guilding, 1829

Type Species: *Chiton spinosus* Bruguière, 1792 (by subsequent designation, Gray, 1847).

Acanthopleura vaillantii de Rochebrune, 1882

Chiton testudo Spengler, 1797: 78 (*nom. nud.*).

Acantopleura (sic !) *vaillantii* de Rochebrune, 1882: 192. Pilsbry, 1894: 97. Nierstrasz, 1906: 514. Winckworth, 1927: 206. Ferreira, 1983: 278; 1986: 226, 231, fig. 17.

Acanthopleura sp. (?) Haddon, 1886: 24.

Acanthopleura haddoni Winckworth, 1927: 206, pl. 28: figs. 1-4. Leloup, 1937: 172, figs. 17-19; 1960: 38. Pearse, 1978: 95, fig. 2. Leloup, 1980: 6. Bosch and Bosch, 1982: 145, fig. Smythe, 1982: 82. Ferreira, 1983: 278; 1986: 226, 227.

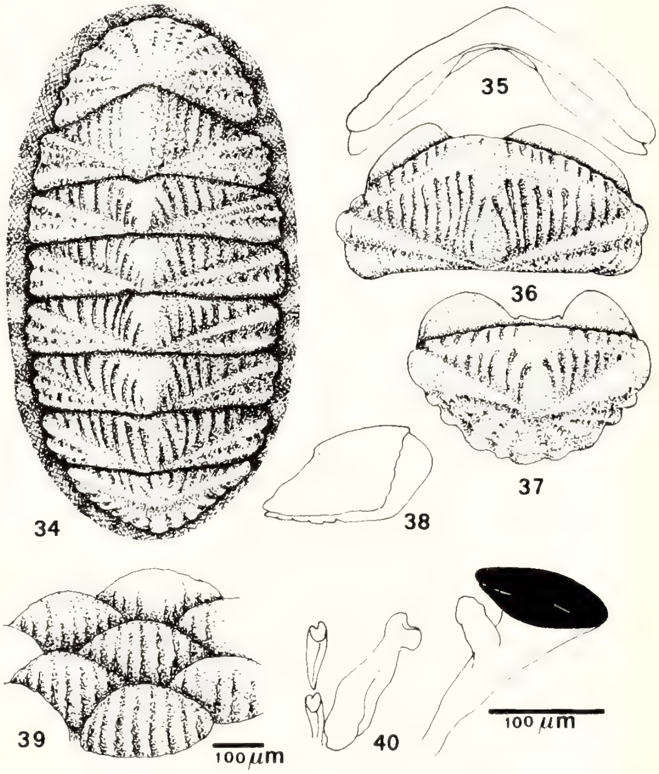
Chiton (Acanthopleura) haddoni, Biggs, 1958: 271; 1969: 201.

LECTOTYPE: MNHN (by subsequent designation, Ferreira, 1986).

TYPE LOCALITY: Suez Canal.

DISTRIBUTION: Red Sea, Yemen, Oman, Arabian Gulf at Jumeira (near Dubay), U. A. E., Khor Khaymah (S of As Shaam), U. A. E., Sharjah (N of Dubay), U. A. E., near Hormuz Id. and the opposite coast of Iran, also "at a point in Bahrain" (K. Smythe, in litt. 3 June 1987), on rocky shores and in rock pools.

DESCRIPTION: Animal large, to 75 mm long, width about 2/3



Figs. 34-40. *Chiton (Rhyssoplax) affinis* Issel. (specimens from Fuwairat, Qatar, June 1985. A. Woodward leg. in coll. Smythe, RMNH K5102). **Fig. 34.** Whole specimen, dorsal view, 6.7 mm wide. **Fig. 35.** Camera lucida sketch of valve IV, rostral view, 3.5 mm wide. **Fig. 36.** Valve IV, dorsal view, 3.5 mm wide. **Fig. 37.** Valve VIII, dorsal view, 2.75 mm wide. **Fig. 38.** Camera lucida sketch of valve VIII, lateral view, 1.94 mm wide. **Fig. 39.** Dorsal girdle scales. **Fig. 40.** Central, first lateral and major lateral radula teeth.

the length, broadly oval, moderately raised, back almost rounded, side slopes slightly convex, valves more or less beaked, generally strongly eroded. Tegmentum dark reddish to blackish brown, some specimens with traces of longitudinal bands of lighter color on jugum.

Head valve nearly semicircular, front slope convex, posterior margin concave in central part, convex toward sides. Intermediate valves broadly rectangular to widely V-shaped, side margins decidedly rounded, apices indicated, blunt, lateral areas little or not raised, hardly marked. Tail valve less than semicircular, crescentic in some specimens, as wide as head valve, mucro somewhat raised, postmedian.

Tegmental sculpture, often indistinguishable on account of erosion and incrustation, consists of small, roundish tubercles arranged in irregular, more or less concentrical rows. Extra-pigmentary eyes very small, abundantly distributed on end valves and more than half of lateral areas of intermediate valves.

Articulamentum glossy, dark brown in central part of valves, light greyish brown toward sides, apophyses large, rounded, somewhat obliquely directed, connected across sinus by short, concave jugal plate, insertion plates short, slit formula 10/1/9-10, slits narrow, inequidistant, slit rays not indicated, teeth finely but deeply grooved on dorsal side, pectinate, those of tail valve slightly directed anteriorly.

Girdle wide, dark brownish, or whitish with irregular dark brown bands, densely clothed dorsally with large, coarse, blunt-pointed, calcareous spines of different forms and sizes, interspersed with small, slender spicules. Marginal spicules more or less cylindrical, almost as long as dorsal spines, blunt-topped, with some wide, longitudinal ribs. Girdle paved ventrally with radiating rows very small, thick scales, slightly longer than wide, squarish at base, distally tapering to blunt top, ornamented with 4-5 strong, longitudinal ribs.

Central tooth of radula slenderly elongate, with broad, strongly convex blade, first lateral tooth irregularly rectangular, major lateral with large unicuspid head, denticle abruptly pointed. Gills holobranchial, abanal.

DISCUSSION: This large, easily recognizable species, was well described by several authors including Haddon (1886), Winckworth (1927) and Leloup (1937). Winckworth produced good figures of the complete animal and the loose valves, and Leloup gave detailed figures of the girdle elements. "*Chiton punctatus L.*" of Spengler (1797:76) is probably a synonym. It was based on animals from the Red Sea, mostly desicated and disarticulated specimens that have lost their girdle armature, leaving deep pits in the cuticula (hence: *punctatus*!). At the end of his description Spengler wrote (p. 78): "The Arabian Society sent it from the Red Sea together with other products of this sea. Due to the similarity of the valves it might be called *Chiton testudo*" (translated from Danish). Although *A. vaillantii* is the only representative of *Acanthopleura* in the Red Sea and Spengler's specimens undoubtedly belong to this genus, there is no certainty about their true identity, so the name *C. testudo* is to be regarded a nomen dubium, leaving *A. vaillantii* the oldest available valid name.

In the opinion of Ferreira (1986), *Acanthopleura vaillantii* should be regarded as another of the many synonyms of *A. gemmata* (Blainville, 1825). Winckworth (1927), however, clearly showed his *A. haddoni* (=*vaillantii*) to be different from *A. spiniger* (Sowerby, 1840) [=*A. gemmata* (Blainville)] in several respects; "in *haddoni* the valves are broader, the diagonal ribs almost obsolete in adult and young specimens, the sculpture is finer abd closer and is uniform over the central and lateral areas, the tail valve is more rounded; the insertion plates and sutural laminae are differently proportioned..."

Leloup (1937: 174) wrote: "The characteristics of the girdle and of the tegmentum as far as the aesthetes are concerned allow us to differentiate *A. haddoni* from *A. spiniger*" (Sowerby, 1840). On the one side the girdle of *spiniger* dorsally bears an underground of uniform, small, brown spicules, which *haddoni* does not show; the thick spines are fairly regularly equal in *spiniger*, whereas they are very irregular in shape and of inequal dimensions in *haddoni*; the scales of the ventral side are relatively longer in *spiniger*. On the other side the aesthetes show the same general aspect, but they are more globulous in *haddoni*, especially in the lateral areas" (translated from French). We agree with the arguments of Winckworth and Leloup and retain *A. vaillantii* as a valid species.

Subfamily Toniciinae Pilsbry, 1893

Genus *Tonicia* Gray, 1847

Type Species: *Chiton elegans* Frembly, 1827 (non de Blainville, 1825) (= *Chiton chilensis* Frembly (1827) (by subsequent designation, Gray, 1847).

Subgenus *Lucilina* Dall, 1882

Type Species: *Chiton confossus* Gould, 1846 (= *Chiton lamellosus* Quoy and Gaimard, 1835) (by subsequent designation, Pilsbry, 1893).

Tonicia (Lucilina) sueziensis (Reeve, 1847)

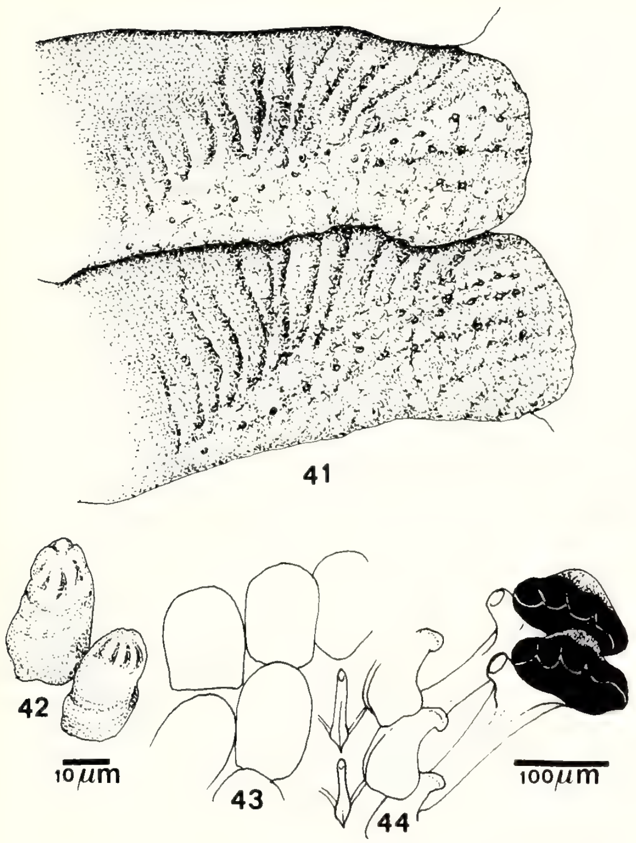
Figs. 41-44

Chiton sueziensis Reeve, 1847: pl. 20, sp. and fig. 134.
Tonicia ptygmata de Rochebrune, 1883: 33. Ferreira, 1983: 274, fig. 28.
Tonicia sueziensis (sic!), Leloup, 1960: 40, figs. 6, 8, pl. 1, fig. 1 (bibliography and synonymy); 1973: 9, 18; 1980: 12.
Tonicia sueziensis, Kaas, 1979: 871. Ferreira, 1983: 271, figs. 25-27; Kaas, 1986: 18.

LECTOTYPE: BMNH 1951.2.7.7 (by subsequent designation, Ferreira, 1983).

MATERIAL EXAMINED: KUWAIT: 2 spec., max. 12 x 7 mm, Bide Circle, under stones in tidepool, F. Hinkle leg., 12 June 1978, FH. —3 spec., max. 9.5 x 6.5 mm, id., 1 Aug 1981, FH; —5 spec., max. 13 x 7.5 mm, id., 10 Apr 1983, FH. BAHRAIN: 1 valve, in shell grit on beach, Nov 1971, F. van Nieulande don., VB 2610a. QATAR: 2 spec., max 9 x 6 mm (slightly curled), Fuwairat, on rocks and dead coral, 0-1 m, June 1985, A. Woodward leg., 1/KS, 1/RMNH K 5102. —1 spec., 22.5 x 8.5 mm, AL Wakrah, on loose rocks covered with algae and weed, 0-1.5 m, June 1984, A. Woodward leg., KS.

DISTRIBUTION: Gulf of Suez, Red Sea, coasts of Somalia, Seychelles Is and Coetivy Id.; Kuwait, Bahrain and Qatar; intertidal to shallow subtidal.



Figs. 41-44. *Tonicia (Lucilina) sueziensis* (Reeve) (specimen from Fuwairat, Qatar, June 1985, A. Woodward leg. in coll. Smythe, RMNH K5098). **Fig. 41.** Right half of valves IV and V in situ, 4.25 mm wide. **Fig. 42.** Dorsal girdle spicules. **Fig. 43.** Ventral girdle scales. **Fig. 44.** Central, first and major lateral radula teeth.

TYPE LOCALITY: Egypt, Suez.

DESCRIPTION: *Tonicia (Lucilina) sueziensis* was adequately described by several authors, particularly Leloup (1960), who produced detailed figures of the girdle elements, and Ferreira (1983), who gave good figures of the lectotype and an accurate description of the radula.

Girdle covered dorsally with extremely minute, bullet-shaped spicules, 36 x 20 μm, top with 4-5 short riblets on visible half; ventral scales (Fig. 43) arranged in lateral rows, rectangular, base slightly concave, top rounded, 25 x 19 μm (Figs. 41-43).

Central tooth of radula (Fig. 44) small, very narrow, 68 x 7 μm, with sharply pointed blade; first laterals broad, base bluntly pointed, pinched in middle, gradually widening distaad, with outwardly directed extension; major laterals with tetracuspid head, denticles short, bluntly rounded, shaft with trunk-like appendix just under and beneath head, directed inward.

DISCUSSION: Ferreira (1983: 274) wrongly synonymized *Tonicia (Lucilina) carnosa* Kaas, 1979, from Mozambique, the Comoro Archipelago, and Madagascar, with the present species. *T. (L.) carnosa* differs considerably in color and in having much weaker sculpture with far fewer longitudinal grooves on central areas of intermediate valves.

Genus *Onithochiton* Gray, 1847

Type Species: *Chiton undulatus* Quoy and Gaimard, 1835. *non* Olfers, 1818; Wood, 1828 (= *Onithochiton neglectus* de Rochebrune, 1881 (by subsequent designation, Gray, 1847).

Onithochiton erythraeus Thiele, 1910

Figs. 45-50

Onithochiton erythraeus Thiele, 1910: 98, pl. 10, figs. 53-55. Leloup, 1941: 13; 1960: 42, 45, 47. Glynn, 1970: 17. Kaas, 1979: 872. Ferreira, 1983: 276-277.

Onithochiton lyelli forma *erythraeus*, Pearse, 1978: 93, 95, fig. 3.

HOLOTYPE: ZMHU.

MATERIAL EXAMINED: OMAN: 1 spec., 16 mm, Arabian Sea, Masirah Id., 12 Jan 1984, D. Bosch leg., KS. —1 spec., length 21 mm, (slightly curled), id., Rassier, 9 Feb 1982, K. Smythe leg., KS. —2 spec., max. width 12.5 mm (both curled), between Rassier and Haql, K. Smythe leg., 1/KS 1/RMNH K5098. —1 spec., length 13 mm (curled), Haql, K. Smythe leg., KS.

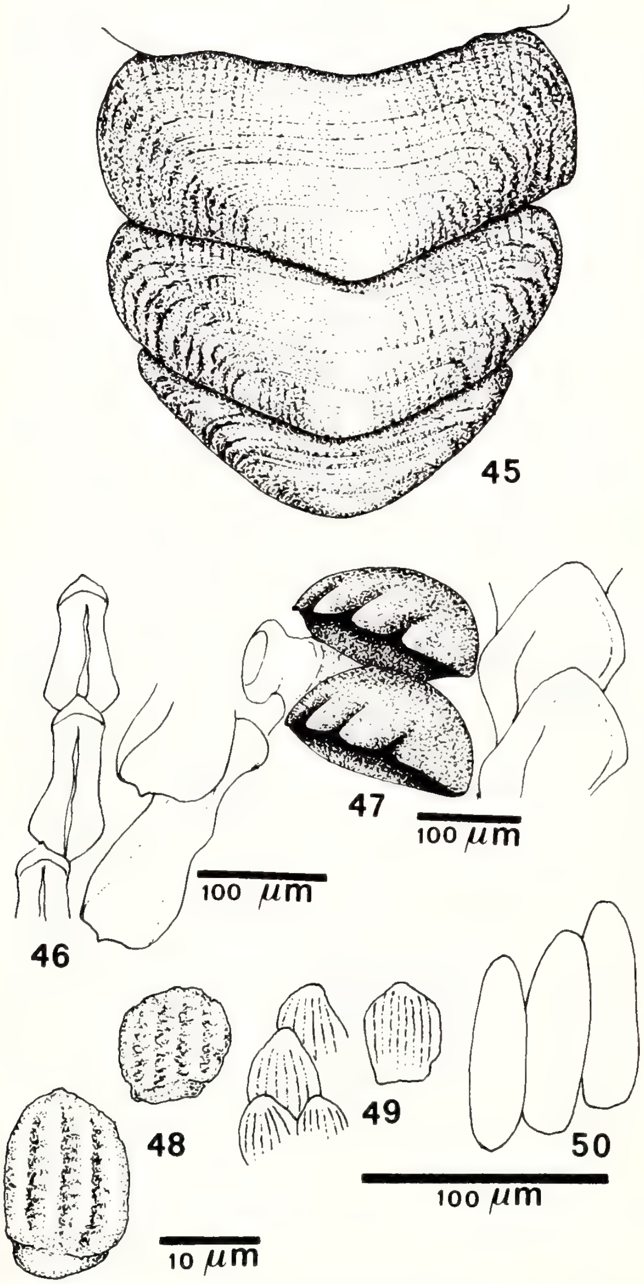
TYPE LOCALITY: Erythraea, El Tor.

DISTRIBUTION: Gulf of Suez, Red Sea, and Arabian Sea coast of Oman; intertidal.

DESCRIPTION: Girdle densely clothed dorsally with tiny, bluntly pointed scales, ca. 23 x 10 μm, top with 5-7 riblets (Figs. 45-49). Marginal spicules (Fig. 50) smooth, cylindrical, bluntly pointed, ca. 90 x 22 μm; ventral scales very small, shorter than wide, ca. 20 x 15 μm.

Central tooth of radula (Figs. 46, 47) about twice as long as wide, widest in anterior part, with extremely narrow, abruptly pointed blade and median, raised riblet in anterior half, base equally pointed; first laterals twice length of central teeth, truncate at base, with central, short, sharp thorn, gradually narrowing anteriorly, ending in narrow, rounded blade; major laterals with tetracuspid head, denticles short, blunt, shaft with short, funnel-shaped appendix just under and anteriorly of head; spatulate uncinal teeth with elongate triangular blade.

DISCUSSION: Though it has not been studied thoroughly before, *Onithochiton erythraeus* has been compared with several related *Onithochiton* species. Leloup (1941) concluded it was synonymous with *O. maillardi* (Deshayes, 1863) from Mauritius. Later, he (Leloup, 1960) considered both of these species, as well as *O. quercinus* (Gould, 1846) from New South Wales, *O. literatus* (Krauss, 1848) from South Africa, *O. wahlbergi* (Krauss, 1848) from the Cape of Good Hope, *O. rugulosus* Angas, 1867 from New South Wales, and *O. scholvieni* Thiele, 1910 from New South Wales, to be junior synonyms of *O. lyelli* (Sowerby, 1832). Ferreira (1983) synonymized *O. wahlbergi*, *O. maillardi* and *O. erythraeus* with *O. literatus*. Kaas (1979) expressed some doubts as to the con-



Figs. 45-50. *Onithochiton erythraeus* Thiele. **Fig. 45.** Valves VI-VIII in situ, dorsal view, 10.3 mm wide. **Fig. 46.** Central and first lateral radula teeth. **Fig. 47.** Major lateral and spatulate uncinal teeth. **Fig. 48.** Dorsal girdle scales from mid-girdle. **Fig. 49.** Same, near outer margin. **Fig. 50.** Marginal spicules.

clusions of Leloup (1960). Pending a thorough study of the type material and good specimens from the different localities, we prefer to treat the matter conservatively and consider *O. erythraeus* a valid species, especially after we were able to compare the Oman specimens with several lots of *O. literatus* from Isipingo, Natal, and Inhaca Id., Lourenço Marques, Mozambique, which proved to be quite differently sculptured.

Suborder Acanthochitonina
Family Acanthochitonidae Pilsbry, 1893
Subfamily Acanthochitoninae
Genus *Acanthochitona* Gray, 1821

Type Species: *Chiton fascicularis* Linnaeus, 1767 (by monotypy).

Acanthochitona woodwardi Kaas and Van Belle, *sp. nov.*

Figs. 51-60

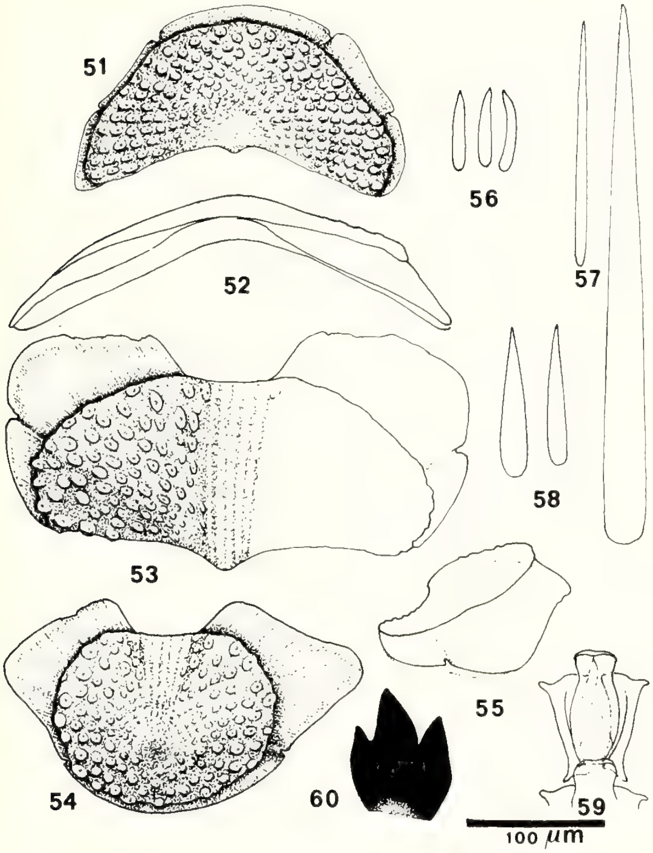
TYPE MATERIAL: HOLOTYPE: 6.7 x 4.0 mm, Qatar, Dasa, 15 Nov 1978, K. Smythe leg., BM(NH) 1987032. PARATYPES: QATAR: 17 spec., max. 9.0 x 4.7 mm, collected with holotype, 13/KS, 2/RMNH K5095 (one disarticulated, figured here), 2/VB 2968b. —2 spec. (curled, one on matchstick) Ras Abruk, 3 Nov 1978, A. Partridge leg., KS. —1 spec. (disarticulated), Ras Abruk, under broken slabs of fasht, intertidal, May 1982, A. Woodward leg., KS. —3 spec., Fuwairat, on rocks and dead coral, 0-1 m, June 1985, A. Woodward leg., 2/KS 1/RMNH K5096. —2 spec. (one juvenile), Al Wakrah, K. Smythe leg., KS. KUWAIT: 2 spec., Al Bide, on rocks in intertidal zone, 29 Jan 1975, B. Glayzer leg., 1/BG 1425 (as *Chiton* sp.), 1/KS (disarticulated, on slide). —2 spec., 5.5 x 3.0 mm (damaged) and 5.0 x 2.5 mm (disarticulated), Bide Circle, under stones in tidepool, MTL, F. Hinkle leg., 12 June 1978, former, FH, latter, VB 2968a. —1 spec., 8.5 x 4.0 mm, id., 1 Aug 1981, FH.

DISTRIBUTION: Kuwait and Qatar; intertidal.

DIAGNOSIS: Animal small, holotype 6.7 x 4 mm, length of largest specimen 9 mm, width about half length, elongate oval, rather flat (dorsal elevation 0.20-0.24), back subcarinate, side slopes straight to slightly convex, head and intermediate valves decidedly beaked. Tegmentum mostly whitish to light beige, speckled or flecked with dark greyish green, some specimens with light brownish or reddish brown, more or less triangular blotch on jugum of valve II, another specimen reddish, shading into roseate to whitish on apical areas, holotype blackish brown, with jugum and girdle whitish. Tegmental sculpture of flat, roundish to oval, neatly separated granules, jugal areas not raised, weakly ribbed longitudinally. Girdle finely spiculose, little encroaching at sutures. Major lateral radula tooth tricuspid.

DESCRIPTION: Head valve (Fig. 51) semicircular, front slope somewhat convex, anterior margin vaguely waved, posterior margin beaked, tegmentum sculptured with neatly separated, flat, roundish to oval, quincuncially arranged granules, larger toward outer margin, smaller, becoming obsolete toward apex, no growth lines. Intermediate valves (Figs. 52-53) twice as wide as long, front margin straight to slightly convex at both sides of concave jugal part, hind margin concave at both sides of strongly protruding apex, jugal area narrowly wedge-shaped, not raised, sculptured with ca. 5 weak, flat, longitudinal ribs separated by very fine grooves, lateral areas not marked but slightly raised with regard to pleural areas, sculpture of latero-pleural areas similar to that of head valve but granules larger, more widely spaced, less regularly arranged. Tail valve (Figs. 54, 55) slightly oval transversely, mucro prominent, pointed, somewhat behind centre, posterior slope strongly concave, tegmentum sculptured like latero-pleural areas of intermediate valves.

Articulamentum whitish, tegmental color slightly visible through, intermediate valves with transverse callus in cen-



Figs. 51-60. *Acanthochitona woodwardi sp. nov.* **Fig. 51.** Valve I, dorsal view, 3.33 mm wide. **Fig. 52.** Camera lucida sketch of valve IV, rostral view, 4.44 mm wide. **Fig. 53.** Valve IV, dorsal view, 4.44 mm wide. **Fig. 54.** Valve VIII, dorsal view, 3.38 mm wide. **Fig. 55.** Camera lucida sketch of valve VIII, lateral view, 1.95 mm. **Fig. 56.** Dorsal girdle spicules. **Fig. 57.** Small and large spicule from sutural tuft. **Fig. 58.** Ventral spicules. **Fig. 59.** Central and first lateral radula teeth. **Fig. 60.** Blade of major lateral tooth. (Figs. 56-60, scale bar = 100 μm.)

tral part, apophyses rounded, sharp, smooth, jugal sinus about 1/5 valve width, weakly concave, insertion plates rather short, slit formula 5/ 1/ 2 (figured specimen with only 4 slits in valve I), slits shallow, slit rays hardly or not indicated, teeth sharp, smooth to very finely striate, eaves solid.

Girdle densely covered dorsally with small, straight to slightly bent, abrupty pointed, smooth spicules, ca. 60 x 10 μm (Fig. 56), sutural tufts relatively short, composed of straight, slender, sharply pointed, smooth spicules of different sizes, varying from 180 x 8 μm to 400 x 30 μm (Fig. 57). Ventral side of girdle paved with close set, radiating rows of sharply pointed, smooth spicules, up to 100 x 20 μm (Fig. 58). Marginal spicules similar to ventral ones.

Central tooth of radula (Fig. 59) elongate tulip-shaped, with thin blade, first lateral tooth somewhat shorter, slender, slightly widening distally, anterolateral corner with sharply pointed outward lobe, no blade, major lateral with tricuspid head, denticles pointed, central one longer than others (Fig. 60).

Gills merobranchial, abanal, 11 ctenidia per side.

DISCUSSION: This species cannot be attributed to any known species in the Indian Ocean. *Acanthochitona mahensis* Winckworth, 1927, from Mahé, India, and *A. ashbyi* Leloup, 1937, from the Indian Ocean (?), possibly a synonym of the former, differ in their greater size, more close packed, coarser granules, finely ribbed jugal areas, relatively wider tail valves with convex postmucronal slope, and longer, coarser, longitudinally striate marginal girdle spicules. In *A. curvisetosus* Leloup, 1960, from the Red Sea, the granules are smaller and more rounded, the jugal areas relatively wider and ornamented with ca. 15 longitudinal striations, and, contrary to those of *A. woodwardi*, the ventral girdle spicules are smaller than the dorsal ones. *A. limbata* Kaas, 1986, from Madagascar, differs in the form of the valves, the drop-shaped granules, the much broader jugal areas, and the form of the major lateral radula tooth.

ETYMOLOGY: This species is named after Mr. A. J. Woodward.

Genus *Notoplax* H. Adams, 1861

Type Species: *Cryptoplax (Notoplax) speciosa* H. Adams, 1861 (by monotypy).

Subgenus *Notoplax* s.s.

Notoplax (N.) arabica Kaas and Van Belle, *sp. nov.*

Figs. 61-72

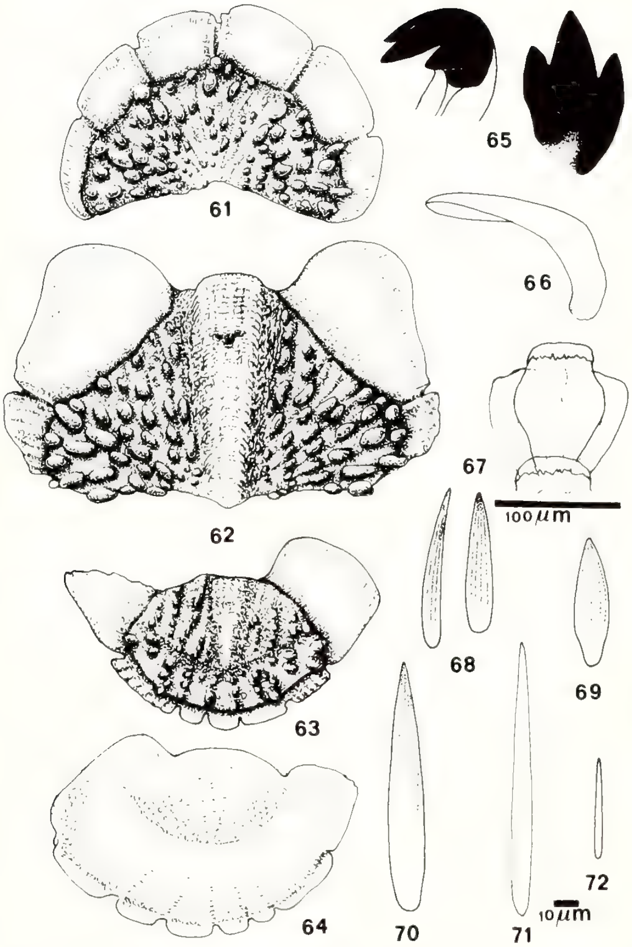
Schizochiton jousseaumei, Smythe, 1982: 84, fig. 18 (non Dupuis, 1917). Glayzer *et al.*, 1984: 324.

TYPE MATERIAL: HOLOTYPE, 11.4 x 5.9 mm, Kuwait Bay, Kuwait, on rocks and dead shells, intertidal, 14 Feb 1975, B. Glayzer leg., BMNH 1987031. PARATYPES: 2 spec., 9.9 x 5 mm and 8.3 x 3.9 mm, collected with holotype, BG 1195. —7 valves (disarticulated), collected with holotype, RMNH K5106. —1 spec., 11.0 x 6.0 mm (disarticulated), Fuwairat, Qatar, on rocks and dead coral, 0-1 m, June 1985, A. Woodward leg., KS.

DISTRIBUTION: Kuwait, Qatar; intertidal.

DIAGNOSIS: Animal small, 10-11 mm long, width about half length, rather flat, side slopes slightly convex, valves little beaked. Tegmentum uniformly light ochraceous, greyish or light orange, coarsely sculptured with large, strongly elevated, radially directed, elongate pustules, jugal areas wedge-shaped, raised, back rounded, neatly separated from the adjacent lateropleural areas by deep, wide grooves. Girdle finely spiculose, deeply encroaching between valves. Major lateral radula tooth tricuspid.

DESCRIPTION: Head valve (Fig. 61) nearly semicircular, front slope weakly convex, anterior margin with five more or less distinct waves, posterior margin widely V-shaped, minutely notched in middle, no trace of radial ribs. Intermediate valves (Fig. 62) broadly triangular, front margin slightly concave at both sides of strong, forwardly produced, convex jugal part, hind margin weakly beaked, somewhat sinuose at sides, apices sharply pointed, lateral areas indiscernible. Tail valve (Figs. 63, 64) very small, transversely oval, mucro prominent, not elevated, slightly postmedian, posterior slope deeply concave.



Figs. 61-72. *Notoplax arabica sp. nov.* **Figs. 61-63.** Valves I (4.0 mm wide) V (5.4 mm wide) and VIII (4.0 mm wide) respectively, dorsal view. **Fig. 64.** Valve VIII, ventral view (4.0 mm wide). **Fig. 65.** Heads of major lateral teeth. **Fig. 66.** Spatulate uncinal tooth. **Fig. 67.** Central and first lateral radula teeth. **Fig. 68.** Dorsal girdle spicules. **Fig. 69.** Marginal spicule. **Fig. 70.** Spicule from sutural tuft. **Fig. 71.** Spicule from girdle bridge. **Fig. 72.** Ventral spicules (Figs. 65-67, scale bar = 100 µm; Figs. 68-72, scale bar = 10 µm).

Tegmentum microscopically granulose, end valves and lateropleural areas of intermediate valves sculptured with large, strongly raised, convex, widely spaced, irregularly oval to decidedly elongate, radially oriented pustules, those near valve margins overhanging or projecting past valve, on some valves pustules vaguely arranged in irregular, longitudinal rows, jugal areas raised, smooth to naked eye, ornamented with extremely fine, longitudinal, beaded riblets, accompanied by shallow, longitudinal excavation on both sides.

Articulamentum slightly translucent, tegmental color shining through, apophyses strongly forwardly produced, rounded, jugal sinus moderately to strongly convex, insertion plates long, slit formula 5/ 1/ 6, slits shallow, those of tail valve inequidistant, slit rays hardly or not indicated, teeth of head and intermediate valves long, sharp, weakly striate dorsally, those of tail valve short, blunt, strongly striate.

Girdle dorsally covered with small, straight to slightly bent, sharply pointed, faintly longitudinally striate spicules, 56-62 µm long, 8-10 µm thick (Fig. 68), on girdle bridges interspersed with long, slender, straight, smooth spicules, 110 x 8 µm (Fig. 71), sutural tufts composed of stout, straight, sharply pointed spicules, 100 x 14 µm, weakly longitudinally striate on distal half (Fig. 70). Marginal spicules (Fig. 69) small, decidedly obese, blunt-pointed, finely longitudinally striate, 52 x 14 µm. Girdle paved ventrally with very small, slender, straight spicules, 40 x 3 µm (Fig. 72).

Central tooth of radula (Fig. 67) tulip-shaped, with straight blade, first lateral tooth somewhat shorter, narrowly aliform, without blade, major lateral with tricuspid head, denticles pointed, central one longer than others (Fig. 65), spatulate uncinal tooth bent, smooth, distal end rounded.

DISCUSSION: By its peculiar sculpture of large, elongate, convex, widely spaced pustules, *N. arabica* differs markedly from all known *Notoplax* spp. in the Indian Ocean, its closest relatives being *N. elegans* Leloup, 1981, from Madagascar, which has a greater number of close set, subcircular, concave granules, *N. alisonae* (Winckworth, MS; Kaas, 1976), from Sri Lanka, which has a much greater number of tear-shaped, flat to slightly concave granules, and *N. coarctata* (Sowerby, 1841), from the Philippines, in which the tegmentum of intermediate valves is flask-shaped.

ETYMOLOGY: The name of this species reflects its presence in the Arabian Gulf.

DISCUSSION

The most striking phenomenon among the present material is the discontinuous distribution of *Lepidozona luzonica*, hitherto known only from Luzon, Philippines, the Java Sea and Singapore. Its occurrence in the Arabian Gulf remains inexplicable except for transport resulting from human intervention via navigation. This is the case with *Chaetopleura angulata* (Spengler, 1797) and *Acanthochitona fascicularis* (Linnaeus, 1767). Another striking fact is the absence of *Chiton huluensis* (Smith, 1903), also discontinuously distributed, covering a vast area from the Tasman Sea through the Torres Straits, the Moluccas, the Timor Sea, the Maldive Islands, Sri Lanka, the western coast of Madagascar, the coast of Mozambique, the Red Sea and through the Suez Canal to the Mediterranean coast of Israel. It should be remembered, however, that the bulk of material we studied was collected in intertidal or shallow subtidal areas, except for some specimens collected in 15-20 m depths by SCUBA.

Ferreira (1983) concluded that "at least as far as chiton faunas are concerned, the tropical western Indian Ocean constitutes a definite zoogeographic province, which includes the Red Sea, the East African coast southward to Natal, and the adjacent islands eastward to Mauritius (60ºE)." Undoubtedly the chiton fauna of the western Indian Ocean is far richer in species than is that of the Indo-Arabian side. However, 50% of the species found in the Gulf and on the Oman coast also are found on the African coast, and all but one also occur in the Red Sea. On the other hand, *Callistochiton adenensis* occurs on the Oman coast as well as in the Red Sea but has not been found in Somalia nor south of there. So we can conclude that the Red Sea chiton fauna is composed both of African and Indo-Arabian species. Nevertheless, a comparison of the faunas of both sides of the Indian Ocean leads to some preliminary conclusions. The genus *Chiton s.s.* is represented by two species on both sides: *C. peregrinus* in the east, *C. salihafui* Bullock, 1972, in the west, and *C. fosteri* on both sides. Two other Indo-Arabian chiton species reach their northern limit in the Gulf, *Ischnochiton winckworthi* and *Lepidozona luzonica. Acanthopleura vaillantii* appears to be the only representative of that genus in the east, whereas it is accompanied by *A. brevispinosa* (Sowerby, 1840) on the African coast. Two species of *Cryptoplax* have been reported from the African coast, of which *C. sykesi* Thiele, 1909, also is found in the Red Sea; none are found on the Indo-Arabian side.

Because of the limited number of chiton species occurring in the northern tropical Indian Ocean, the distribution data reviewed here do not allow zoogeographic provinces to be established.

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SENSE ORGANS IN THE GIRDLE OF *CHITON OLIVACEUS* (MOLLUSCA: POLYPLACOPHORA)

FRANZ PETER FISCHER, BRIGITTE EISENSAMER, CHRISTINA MILTZ
AND **INGRID SINGER**
INSTITUT FÜR ZOOLOGIE, TECHNISCHE UNIVERSITÄT MÜNCHEN
LICHTENBERGSTRASSE 4, D 8046 GARCHING,
FEDERAL REPUBLIC OF GERMANY

ABSTRACT

A general scheme for the girdle sense organs in the Polyplacophora is put forward: a sensory papilla, inserted in the girdle epithelium, consists of a varying number of secretory cells, one ciliary cell and one spicule cell. The spicule cell is connected with an organic cup or shaft. In or on top of this structure there is a calcareous element (spicule, scale or small tip). The ciliary cell invaginates into the spicule cell. Around this invagination the cytoplasm of the spicule cell contains a dense network of microfilaments and a large number of mitochondria.

Modifications of this scheme are found in *Chiton olivaceus.* Behavioral experiments demonstrate that the girdle sense organs are mechanoreceptors.

The presence of sense organs (aesthetes and shell eyes) in the shell valves of chitons has been known since the work of Moseley (1884). The occurrence of sensory structures in the girdle that surrounds the valves has only recently been demonstrated (Haas and Kriesten, 1975; Fischer *et al.*, 1980; Leise and Cloney, 1982; Leise, 1986). Previously, the hard structures of the girdle were considered as armament and ornamentation by most authors. However, Blumrich (1891) and Plate (1898, 1902) suggested that some girdle formations could be sensory. The ventral and dorsal surface differ in arrangement and form of these structures, differences which are species-specific. In addition, many species have different spines along the girdle margin. In several families, hair-like structures are also produced. A survey of the different forms is given in Hyman (1967). Hyman also suggests that hairs could be modified shafts of spicules.

The ultrastructure of the girdle is still poorly known. With the exception of *Lepidochitona cinereus* L. (Haas and Kriesten, 1975), the species that have been studied, *Acanthochitona fascicularis* L. (Fischer *et al.,* 1980) and *Mopalia muscosa* Gould (Leise and Cloney, 1982; Leise, 1986), have a highly specialized girdle.

This study concerned *Chiton olivaceus* Spengler, the most common chiton in the Adriatic Sea; it is dominant in the tidal and low subtidal region (Leloup and Volz, 1938). The girdle ornamentation has been described by Blumrich (1891) and no obvious specializations exist. We examined the ultrastructure of both scales and hairs in order to reveal the basic structure of the girdle sense organs.

MATERIAL AND METHODS

One to three year old individuals of *Chiton olivaceus* from the tidal zone of the coast of northern Yugoslavia were used in this study. For transmission electron microscopy, parts of the girdle were fixed in 5% glutaraldehyde in phosphate buffer (pH 7.4) for two hours. They were then decalcified in 3% EDTA in phosphate buffer overnight following postfixation in 2% osmium tetroxide for two hours. All this was done at 3°C. After dehydration (ethanol, propylene oxide) the specimens were embedded in Durcupan and ultrathin sections cut with a Reichert ultramicrotome. The sections were stained with uranyl acetate and lead citrate using the standard methods of Reynolds (1963) and studied in a Jeol electron microscope.

For scanning electron microscopy, some specimens, after complete dehydration in a graded series of ethanol, were critical point dried (Balzers CPD 020) from liquid carbon dioxide. Specimens were then coated with a 300 Å layer of gold and viewed in a Jeol 25S SEM.

In order to qualitatively test the reactions of the animals to touching of single spines or other formations of the girdle, a glass microelectrode filled with 3M KCL was connected via a preamplifier to an audiomonitor. Because the sound frequency changes due to a change in resistance of the

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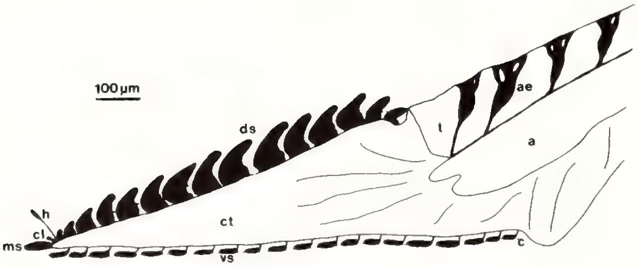


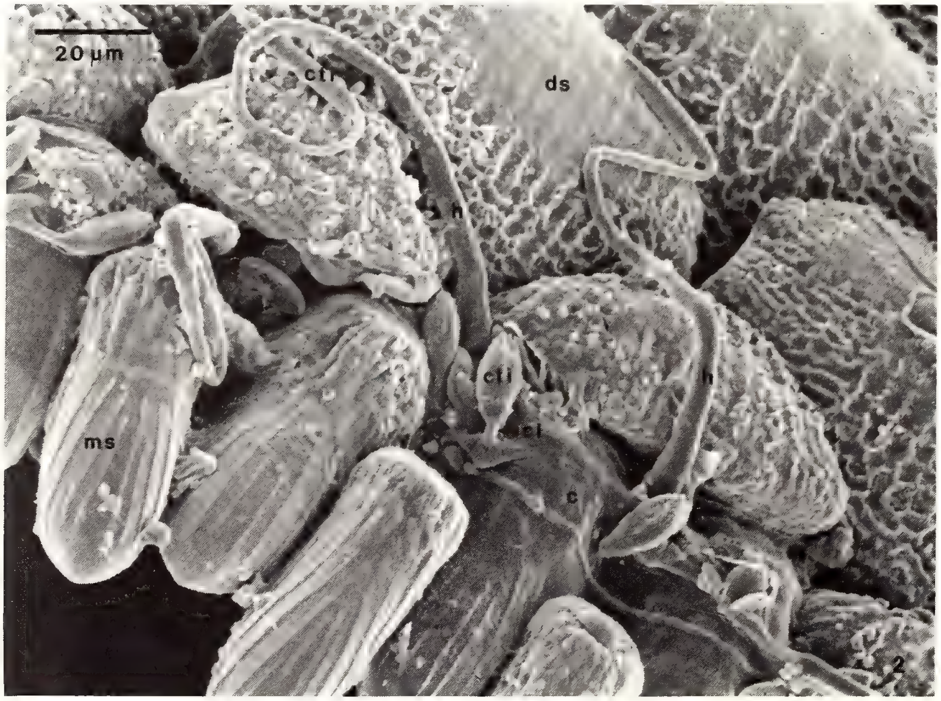
Fig. 1. Schematic cross section through the girdle (a, articulamentum; ae, aesthetes in the tegmental shell layer; c, cuticle; cl, clapper; ct, connective tissue; ds, dorsal scales; h, hair; ms, marginal spines; t, tegmentum; vs, ventral scales) (after Maile, 1981).

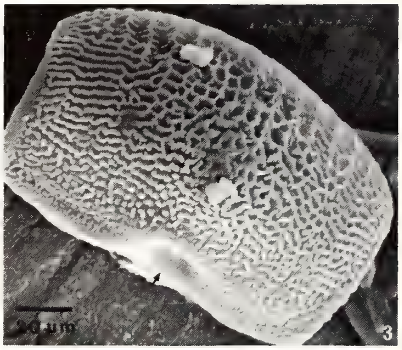
electrode at the very first contact, general pressure on the girdle, instead of the touch of single elements in the girdle, can be excluded as a cause of the observed reactions, e.g. avoidance behavior. The reactions were classified into four categories of increasing intensity: movement of touched element; movement of neighbouring elements; girdle movement near the touched place; whole animal moving away. The frequencies of these avoidance behavior patterns were determined by direct observation. Each of 20 animals was tested several times (depending on the overall activity, that can make the tests quite difficult) and in all areas (dorsal scale, marginal spine, hair, ventral scale). The chitons were light-adapted for at least one hour [dark-adapted animals exhibit a marked response to light (Bergmann, 1986)]. The chitons had been kept in aquaria containing artificial sea water (20°C, natural day/night-cycle, simulation of high and low tides) for 6 months up to 3 years before the tests.

RESULTS

MORPHOLOGY OF THE GIRDLE

The girdle of *Chiton olivaceus* is covered with characteristic calcareous parts (Fig. 1). On the dorsal surface, large scales are arranged like tiles on a roof, with the open side directed towards the shell. The tallest scales (up to 180x130 μm) are found in the middle part of the girdle, whereas those near the girdle margin and near the shell valves are much smaller (50x20 μm). In most cases, the surface of the scales shows irregular elevations and ridges (Figs. 2, 3). The girdle margin is formed by one row of calcareous spines (50-90 μm long and 20-25 μm wide). They bear thin ridges running roughly parallel to their long axes (Fig. 2). Between the marginal spines and the dorsal scales, hair-like formations can be observed at regular distances. One hair is normally accompanied by one or two clapper-like structures. Each hair or clapper consists of a solid shaft of organic material and a calcareous tip, which can be lost in some hairs. The hair shaft is 70-110 μm long and between 5 μm (at the base) and 1.5 μm wide (distally). The calcareous tip structure can reach a length of 30 μm and a diameter up to 4 μm. The organic shaft of the clappers is 10 μm long and 2 μm wide; the calcareous tip is 10-15 μm long and about 7 μm in width.





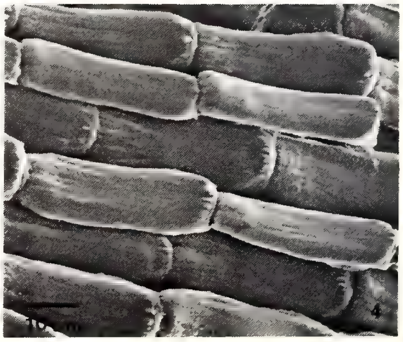


Fig. 2. Scanning electron micrograph of the girdle margin (cl, clapper; cti, calcareous tip of a hair or clapper; c, cuticle; ds, dorsal scale; h, hair; ms, marginal spine). **Fig. 3.** Isolated dorsal scale, KOH-treated. A groove (arrow) shows the connection site with the spicule cell of the papilla. **Fig. 4.** Ventral scales (right side is lateral).

In living animals, the hairs are straight and oriented at an angle between 0º (parallel to the substratum) and 60º. Ventrally, the girdle is covered with rows of small scales (30-40 μm long, about 13 μm broad) (Fig. 4). The rows are oriented perpendicular to the girdle's margin. All scales, at least at their base, are embedded in the cuticle.

AVOIDANCE BEHAVIOR OF LIVING ANIMALS

We studied qualitatively the avoidance behavior of 20 individuals of different ages (age can be estimated from the size of the animals). There was no difference in the reactions between these chitons.

Generally, there is a reaction to touch of any calcareous element but of a varying degree (Table 1). Girdle movements in the stimulated region can be observed upon touch of every structure. However, the weak reaction of the dorsal scales and the hairs could be accidental, as girdle movements can sometimes be registered without obvious external stimulation. Individual ventral scales are not moved. They are embedded in the cuticle except at their distal surface. The most effective stimulation is contact of a marginal spine. The touched spine is moved away immediately with a subsequent movement of neighboring spines. The girdle in the stimulated areas is withdrawn and, after repeated stimulation the animal often moves away. The reaction of the other structures to touch is much weaker; the weakest is that of the hairs.

Because the clappers are very small and inserted very close to the hairs, it was not possible to stimulate this structure without also possibly stimulating a hair. Therefore, the clappers were omitted in Table 1.

PARENCHYME OF THE GIRDLE

The parenchyme of the girdle consists of a network of connective tissue (Fig. 5). The nuclei of these cells are relatively small. The space between the cells is filled with irregular groups of collagen fibers and scattered muscle cells. The muscle cells insert at the basal lamina of the epidermis and not at the hard structures of the girdle. The movement of spines is obviously produced indirectly by contraction of the underlying muscle cells. Hemolymph filled lacunae of various sizes are bordered only partially by the cells of the connective tissue; they continue to a large extent into the intercellular substance.

Table 1. Avoidance behavior of *Chiton olivaceus* upon touch of single elements in the girdle with a glass microelectrode (– = no reaction observed, + = up to 30% of the tests were positive, ++ = 30-60% of the tests were positive, +++ = > 60% of the tests were positive). The ventral scales tested were in girdle areas which were not completely attached to the substratrum. Altogether, 60 tests were performed for each of the girdle elements, except for the ventral scales (31 tests).

	movement of touched element	movement of neighboring elements	girdle movement	animal moves away
dorsal scale	+	–	+	–
marginal spine	+++	++	+++	++
hair	–	–	+	–
ventral scale	–	–	++	–

EPIDERMIS

The girdle epidermis consists of 2.5-4.5 μm high cells that are intensively interdigitated. Distally, the epidermal cells are connected by zonulae adhaerens and septate junctions. Short microvilli (0.5-1 μm in length) protrude into the cuticle. The nucleus fills most of the cell's volume; its chromatin is highly condensed, a sign of relatively low metabolic activity. Many tonofilaments run from the basal lamina up to the tips of the microvilli (Fig. 6). Scattered ribosomes and only a few mitochondria are also found randomly in the epidermal cells. In areas where new papillae are formed, epidermal cells show ultrastructural features indicating higher metabolic activity. They have a larger cell volume, the chromatin is less condensed and the cytoplasm contains more mitochondria and some endoplasmic reticulum (ER). There is a regular transition to the secretory cell type of the papillae.

GENERAL PATTERN OF THE GIRDLE PAPILLAE

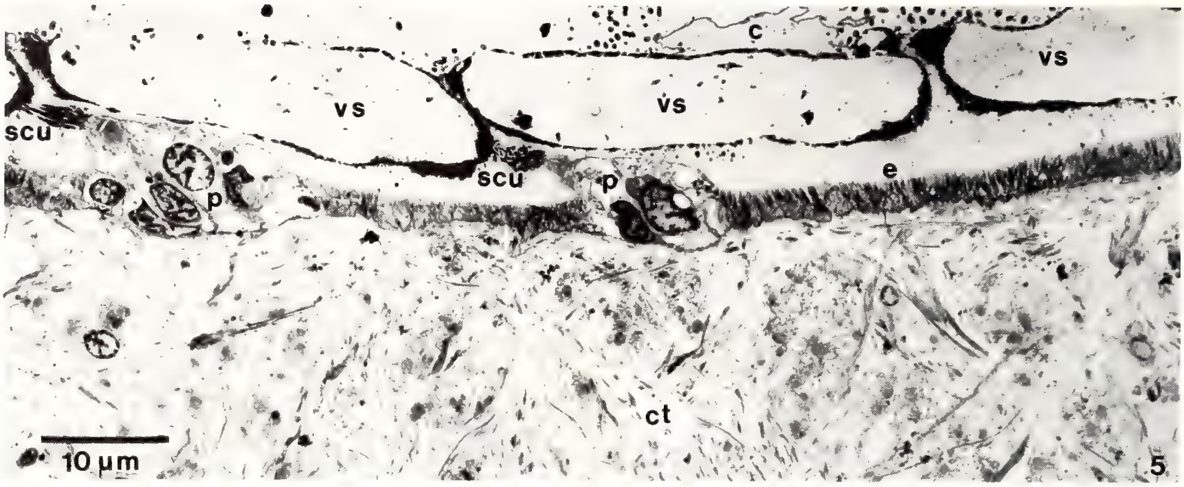
Papillae of various sizes (according to the position on the girdle) insert in the epithelial layer. Generally, a papilla contains a varying number of secretory cells, one ciliary cell and one spicule cell. The external appearance of the formations on the girdle looks very different (Fig. 2). However, the composition of the papillae (which are connected with these formations) is essentially the same. Therefore, a detailed description of the cell types found in a papilla is next described.

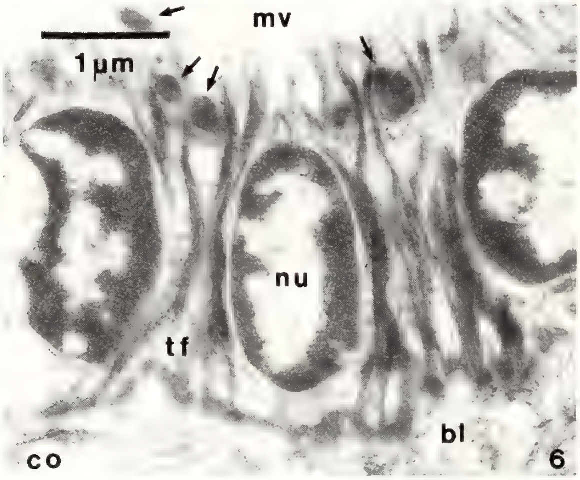
SECRETORY CELLS

Secretory cells, as well as all other cells of the papilla, are interconnected in the same way as the epidermal cells. Active secretory cells have a relatively large nucleus without much condensed chromatin which normally lies near the basal lamina. Granular ER, free ribosomes and numerous mitochondria are a regular feature of the cytoplasm. Golgi apparati are rare, although the cell is filled to a large extent with membrane-bound secretory granules. Other granules, of varying electron density, and a few multivesicular bodies are also found. In older papillae, especially at the ventral side of the girdle, the secretory cells' activity decreases and the chromatin becomes more condensed (new papillae are formed mainly near the shell and the girdle margin, dorsally and ventrally the zone between these areas contains older papillae except in places where a scale had been lost.

CILIARY CELL

The ciliary cell also shows the ultrastructural features of high metabolic activity. The large nucleus is surrounded by granular ER; many mitochondria, a few granules and multi-





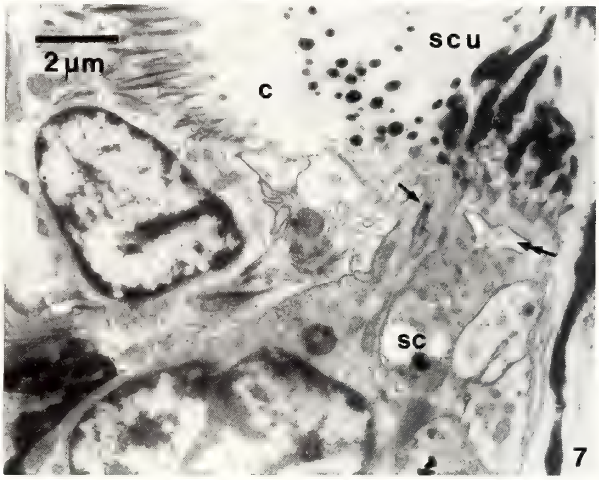


Fig. 5. Cross section through the girdle, ventral part. Two papillae (p) are connected by cups with their scales (ct, connective tissue; c, cuticle; e, epidermis; scu, spicule cup; vs, ventral scale (decalcified) (left is lateral, upper side is ventral). **Fig. 6.** Epidermis on the dorsal side of the girdle (bl, basal lamina; co, collagen; mv, microvilli; nu, nucleus; tf, tonofilaments; arrows indicate branches of the cup of a dorsal scale running down between the microvili of the epidermal cells). **Fig. 7.** Distal part of a ventral papilla (c, cuticle; sc, spicule cell; scu, spicule cup). A cilium protruding from the ciliary cell can be seen (arrow). This cell invaginates into the distal part of the spicule cell (double arrow).

vesicular bodies are also present. Distally, the cell is elongated and protrudes up to the cuticle. Relatively large (0.5 μm in diameter) microvilli protrude into the cuticle. One cilium (9+2 structure) runs to the base of the spine, scale, clapper or hair (in these sections we refer to all these formations as "spicules") (Fig. 7). This cilium originates from a striated rootlet that consists of several parts (Fig. 8). Branches of the ciliary cell invaginate into other cells, especially into the distal area of the spicule cell (Figs. 9, 10). Two centrioles are present in this invagination. In longer papillae, the distal part of the ciliary cell contains many microtubules. This zone then resembles a dendrite.

SPICULE CELL

The spicule cell connects the spicule with the papilla. Again, the nucleus is large and does not contain much condensed chromatin. Especially in the distal half of the cell agranular ER, numerous microtubules and many mitochondria are present. This zone is also characterized by the invagination of the ciliary cell mentioned above. The membranes of both cells are parallel to each other, and the spicule cell forms a dense network of microfilaments around this part of the ciliary cell (Fig. 9). Distally, the spicule cell bears numerous microvilli that are connected with the organic cup or shaft of the spicule (Fig. 11). The calcareous element is placed in or on top of this organic structure. It does not contain any cellular elements. In all parts of the girdle, the cilium of the ciliary cell at the base of the spicule is oriented towards the girdle margin, i.e. the papillae are polarized. Structures resembling small neurons (fibers containing numerous microtubles) can be found from the basal lamina far up into the papilla. However, no synapse or direct connection to a cell could be seen so far.

VENTRAL PAPILLAE

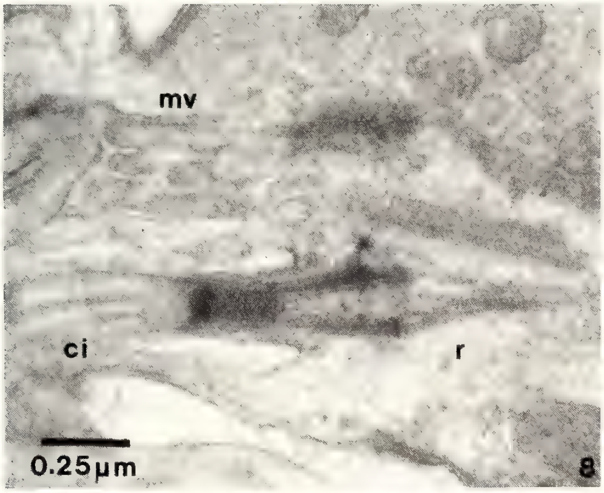
The ventral papillae are oriented at an angle of 10-20°

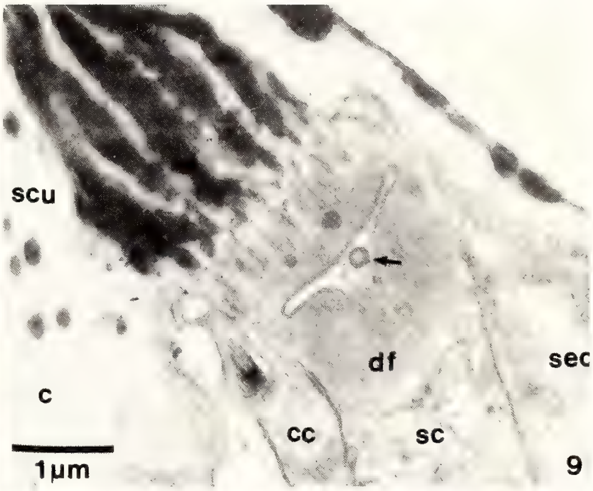
towards the girdle margin (Figs. 5, 12). A papilla consists of about seven cells (one spicule cell, one ciliary cell and about five secretory cells). The cup of the ventral scale consists of three zones. The proximal filaments are very thin (about 15 nm; in the median zone these filaments become thicker (150 nm). The area adjacent to the calcareous scale is homogeneous and surrounds the scale continuously in younger scales; in older ones the distal parts of the organic component has been eroded. Newly formed scales lie near the papillae, older ones have moved far into the cuticle. In these papillae the ciliary and spicule cells are elongated up to the scales' cup. Finally, the scale is dropped and a new one is formed (for a description of the formation of spicules see Haas and Kriesten, 19795).

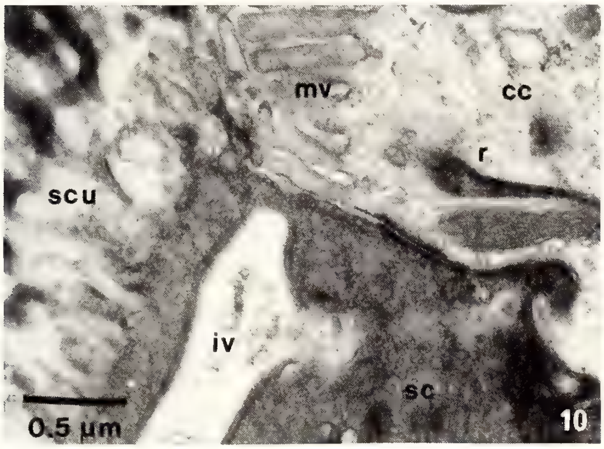
DORSAL PAPILLAE

The size of the papillae on the dorsal side of the girdle varies considerably. They are small near the margin and the shell valves, where the scales are also small, and very large in the median area of the girdle. In this median area one cannot clearly distinguish between distinct papillae; a large scale can be surrounded by a ring of papillae-like cell complexes. Only on one side, towards the shell valve, are the spicule cell and the ciliary cell present (Fig. 11). Underneath the scale, normal epidermal cells are present (Fig. 13). All other cells are of the secretory type (Fig. 14).

The cup of a dorsal scale is composed of two parts (Fig. 15). In most cases the basal plate has a straight border towards the calcareous element; at the lower side, short branches run down between the microvilli of the epidermal cells (Fig. 6). At the lateral side, the scale is covered with an organic sheet that reaches the basal plate; there is often no direct connection between these two parts. The lateral part has a straight border towards the cuticle and many processes into the calcareous element. In new dorsal scales the basal plate is formed some time after the lateral part.







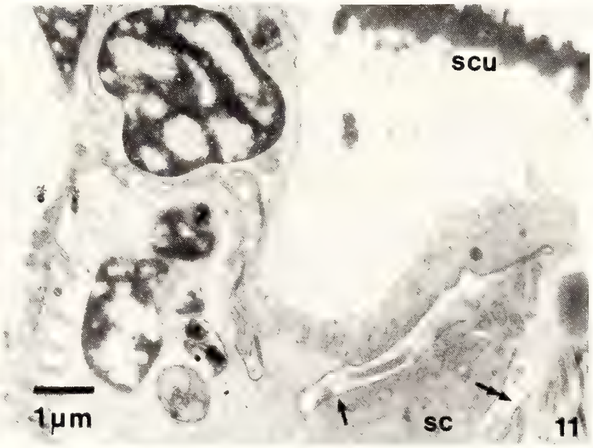


Fig. 8. Longitudinal section through the base of a cilium of the ciliary cell (ci, cilium; mv, microvilli of the ciliary cell; r, striated rootlet of the cilium). **Fig. 9.** Distal part of a ventral papilla (c, cuticle; cc, ciliary cell; df, dense network of small fibers around the invagination of the ciliary cell; sc, spicule cell; scu, spicule cup; sec, secretory cell; arrow indicates basal body). **Fig. 10.** Tips of the ciliary cell and the spicule cell (cc, ciliary cell; iv, invagination of the ciliary cell into the spicule cell; mv, microvilli; r, striated rootlet of a cilium; sc, spicule cell; scu, spicule cup). **Fig. 11.** Section through the receptive part of a dorsal papilla (sc, spicule cell; scu, spicule cup; arrow indicates invagination of the ciliary cell into the spicule cell; double arrow indicates ciliary cell).

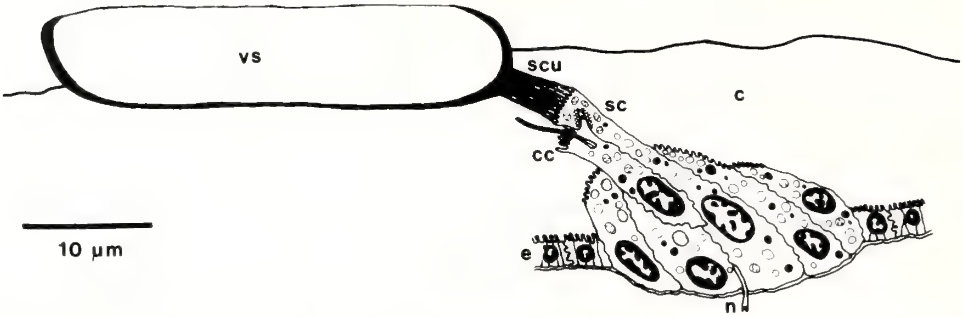


Fig. 12. Schematic drawing of a ventral papilla with its scale. Left side is lateral, upper side is ventral (c, cuticle; cc, ciliary cell; e, epidermal cell; n, neurite; sc, spicule cell; scu, spicule cup; vs, ventral scale;).

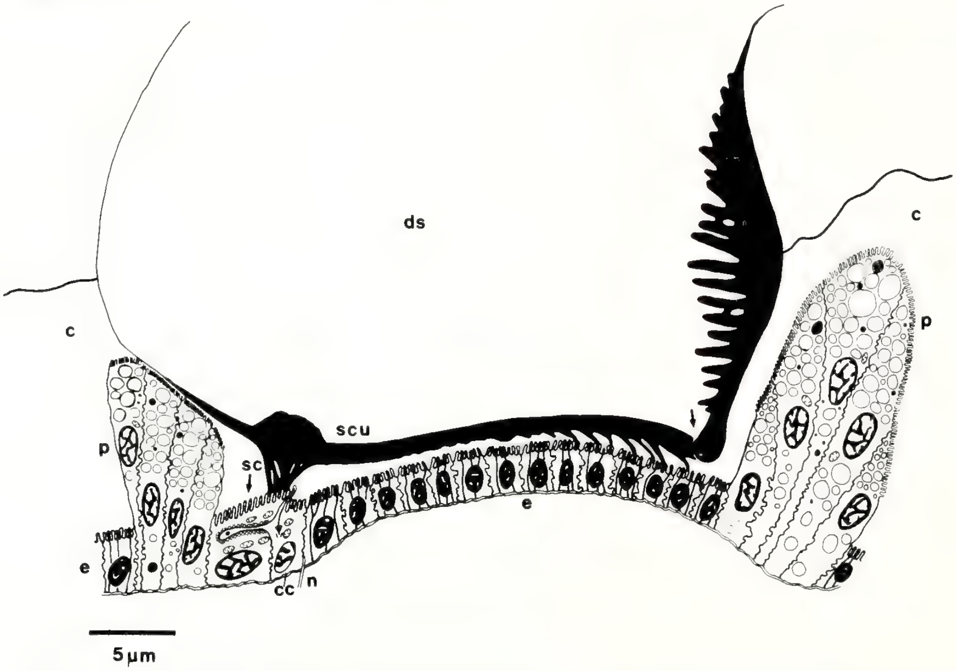


Fig. 13. Schematic drawing of a dorsal papilla complex with its scale [c, cuticle; cc, ciliary cell; ds, dorsal scale; e, epidermal cells; n, neurite; p, papilla; sc, spicule cell; scu, spicule cup); arrow indicates the two parts of the cup of the dorsal scale are attached to each other (right side is lateral)].

GIRDLE MARGIN

The greatest variety of structures is found in the girdle margin. The papillae of the marginal spines, of the hairs and the clappers are in many cases not distinct. All cells at the margin (except spicule and ciliary cells) resemble secretory cells; there are no typical epidermal cells.

At the margin, the papillae lie in three rows: ventrally, the papillae of the marginal spines; medially, the papillae of the clappers; dorsally, the papillae of the hairs (Fig. 16). The papilla of a marginal spine has numerous secretory granules concentrated in the upper side, whereas the papilla of a clapper has most of these granules in its lower side. The cup of the marginal spines consists of the same zones as in the ventral scales. In the clappers, the cup has been transformed into an elongated shaft, which is solid except near the tip of the spicule cell. Around the distal part of the papilla and the base of the shaft, a cortex of darkly stained granules is embedded in the cuticle. The middle zone of the papilla of a hair is quite narrow. All cells, spicule cells and ciliary cells as well as secretory cells, have a thin diameter in this zone. Numerous microtubles contribute to the dendritic appearance (Fig. 17). The distal part of the papilla is swollen (Fig. 18). Secretory cells are highly vacuolized around the spicule and ciliary cells. The hair shaft is solid except at the connection with the spicule cell. The distal (swollen) part and the base of the shaft, as in the clappers, are surrounded by a granulate cortex; in the hairs, it can protrude out of the cuticle for a short distance.

DISCUSSION

Despite the very different external appearance of the girdle formations, all papillae in *Chiton olivaceus* are of similar construction. They are composed of a varying number of secretory cells that surround one spicule cell and one ciliary cell. The ciliary cell invaginates into the spicule cell which is highly specialized in this zone. The spicule cell is connected with the organic cup of a calcareous structure. Both these components vary considerably in size. The same pattern is also found in the primitive polyplacophoran *Lepidopleurus cajetanus* Poli (Fischer, unpublished) as well as in *Lepidochitona cinereus* (Haas and Kriesten, 1975). In *Acanthochitona fascicularis* a similar appearance has been found (Fischer *et al.,* 1980) with three major differences: the secretory cells are more prominent; photoreceptor cells are present in many papillae; a stalked nodule protrudes from many papillae into the cuticle. This nodule resembles the swelling of the hair papilla in *Chiton olivaceus.* It looks like a distal part of a papilla that has lost its spicule. In young *Mopalia muscosa* a pattern similar to *Chiton olivaceus* is found (Leise, 1986) (Fig. 6). It seems that the type described here is the basic structure of the girdle sense organs in the polyplacophora.

In *Acanthochitona fascicularis*, another type of spine has also been described, in addition to this general type. These spines are not connected with a papilla. Each is based on top of a large cup-like cell in the epidermal layer and grows basally as the animal gets larger. In contrast, the "normal" type of spine does not grow after it is produced. Behavioral observations and the fine structure of the cup-like cell suggest that this spine type in *A. fascicularis* is merely defensive (Fischer, 1979).

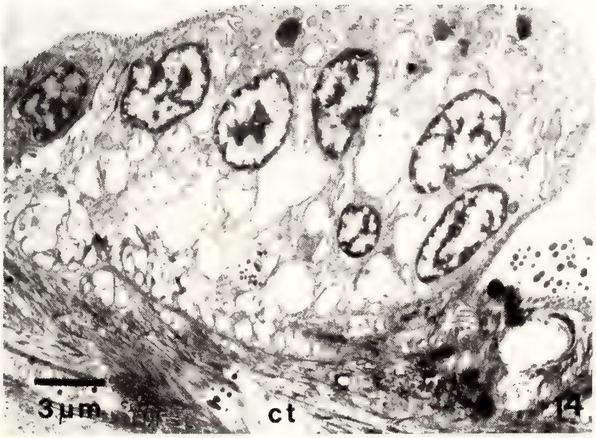
Adult mopaliid chitons have elaborate sensory hairs in the girdle (Leise and Cloney, 1982; Leise, 1986). Leise (1986) has demonstrated that these hairs are formed by the growth of several spines (very similar to the hairs of *Chiton*) close to one another. As they grow, the whole bundle is surrounded by an organic cortex. Thus, the complex hair in *Mopalia* is an elaboration of the "normal" type.

In *Acanthochitona fascicularis* the spicule cell forms a neurite (Fischer *et al.,* 1980). Nerves have also been demonstrated in the girdle sense organs of *Mopalia muscosa* (Leise and Cloney, 1982; Leise, 1986). In *Chiton olivaceus,* structures resembling neurons are present in the papillae of every type of girdle formation. However, the presence of such structures seen in the electron microscope is only an indication of a sensory function, for two reasons. Cells that are not sensory, such as the secretory cells in the aesthetes, can form fiber-like extensions that are very similar in structure to neurons. However, they certainly have another function, as they are not connected with the nervous system (Knorre, 1925). If the fibers observed in the papillae are nerves, they could have other functions such as stimulating the secretory cells. To establish a sensory function, appropriate neurophysiological or behavioral experiments must be carried out. Neurophysiology in chitons is very difficult, as single nerve fibers are thin and the amplitude of potential changes is quite low (Fischer *et al.,* unpub. data).

The results of the stimulation experiments show that the girdle sense organs are mechanoreceptors. Due to the fact that the basic structure is the same in all species and in all areas in *Chiton*, we suggest that, apart from the function of the secretory cells, mechanoreception is the basic function of the girdle papillae. A possible function of the secretory cells could be to produce or impregnate the cuticle. The chemical composition of the secretory granules is unknown.

The presence of mechanoreceptors is certainly of great importance for a relatively small animal which lives in the tidal region and moves actively, but slowly, on exposed substrata for feeding. Individuals of *Chiton olivaceus* which have been detached from their stone have great difficulty settling again in turbulent water (pers. obs.). Under normal conditions, the girdle is pressed onto the substratum. There is no gap and the animals are not vulnerable to strong water movement. The ventral scales could provide feedback information about the pressure of the girdle on the substratum. The reactions to stimulation of the marginal spines show that these structures can detect an obstacle or movements of other animals.

Most chitons including *Chiton olivaceus* do not possess eyes. The photoreceptor cells in the aesthetes (Fischer, 1978) are involved in the photonegative behavior (Arey and Crozier, 1919; Boyle, 1972; Bergmann, 1984) and in the shadow



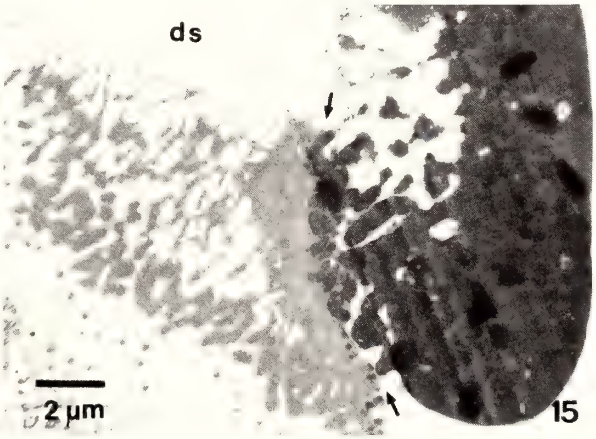


Fig. 14. Section through a dorsal papilla showing secretory cells (ct, connective tissue). **Fig. 15.** Cross section through a part of the cup of a dorsal scale. The border between the basal plate (left) and the lateral part (right) is clearly seen (arrows) [ds, dorsal scale (decalcified)].

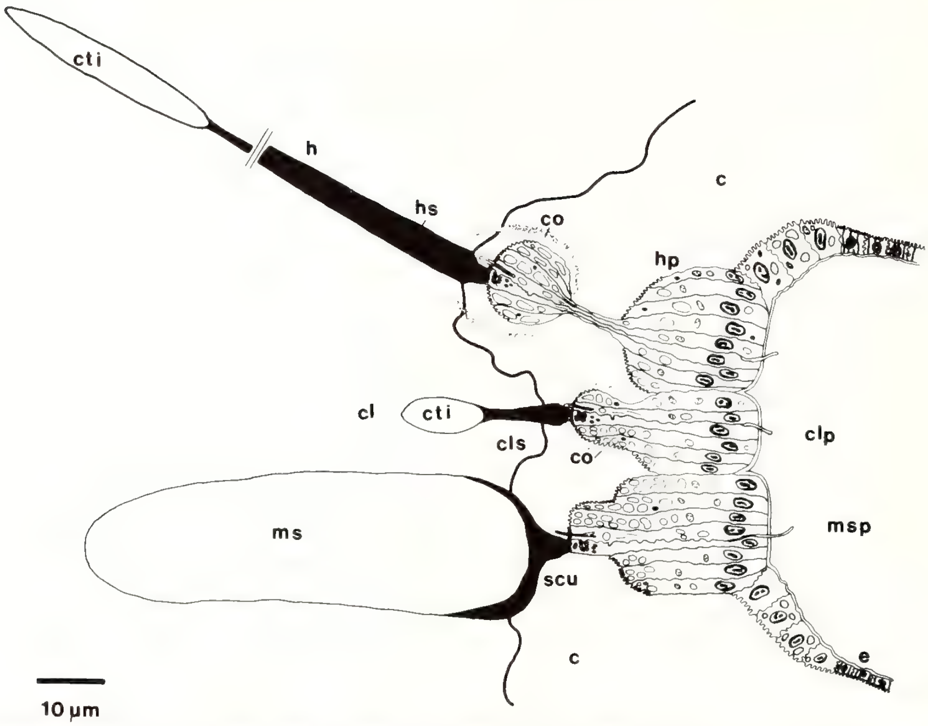
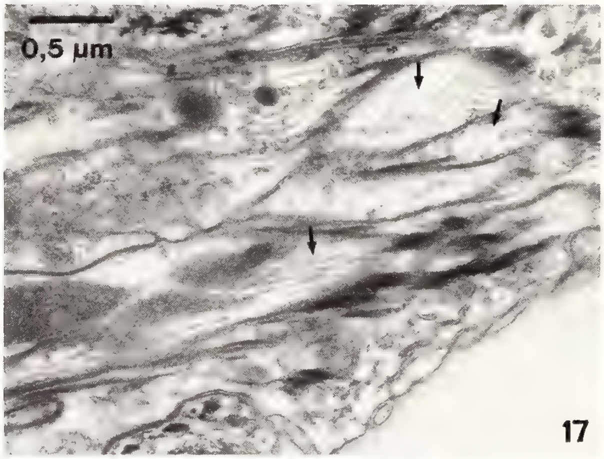


Fig. 16. Schematic drawing of the margin of the girdle [c, cuticle; cl, clapper; clp, papilla of a clapper; cls, clapper shaft; co, cortex-like structure; cti,, calcareous tip of a hair or a clapper; e, epidermis; hs, hair shaft (a specialized spicule cup); h, hair; hp, papilla of a hair; ms, marginal spine; msp, papilla of a marginal spine; scu, spicule cup].

response (Crozier and Arey, 1918). As mainly nocturnal animals, the light sense is not very specialized in chitons. *C. olivaceus* is frequently found on very irregular substratum. They hide in small holes (such as produced by the clam *Lithophaga lithophaga* L.) in stones. The great number of lateral mechanoreceptors obviously is involved in orientation.

Stimulation of the hairs does not evoke a strong reaction, touch apparently being not the appropriate stimulus. When the animal is feeding, the hairs are oriented towards the open water and are moved slightly by water motions (pers. obs.). A possible function could be to measure these movements.

The large dorsal scales certainly protect the animal against predators or strong water movement. Most predators usually only consume the foot and the viscera, not the valves and the girdle (Leise, 1986). When disturbed, *Chiton olivaceus* presses the girdle to the substratum very tightly. It is difficult to detach the animals. For nearly all possible predators, this species is unattractive because of the protection afforded by the valves and the dorsal scales. However, the dorsal papillae still retain the sensory elements, although they are relatively small. Further experiments must be carried out to define the exact function of the girdle sense organs of chitons.



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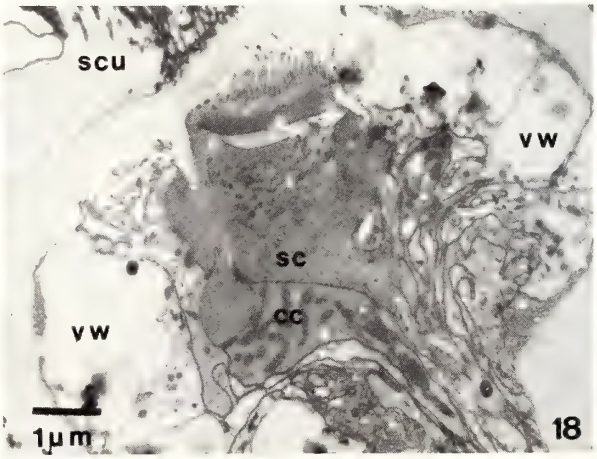

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Fig. 17. Dendrite-like appearance of different cells (arrows) in the base of the distal part of hair papilla. **Fig. 18.** Distal part of a hair papilla [cc, ciliary cell; sc, spicule cell; scu, spicule cup (here transformed into the shaft of the hair); vw, vacuolated secretory wall cells].

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SENSORY ORGANS IN THE HAIRY GIRDLES OF SOME MOPALIID CHITONS

ESTHER M. LEISE[1]
DEPARTMENT OF ZOOLOGY
UNIVERSITY OF WASHINGTON
SEATTLE, WASHINGTON 98195, U. S. A.
and
FRIDAY HARBOR LABORATORIES
FRIDAY HARBOR, WASHINGTON 98250, U. S. A.

ABSTRACT

The polyplacophoran mantle secretes the shell plates, houses the gills in the pallial grooves, and forms a muscular perinotum or girdle that encircles the shell and viscera. The epidermis of this girdle occurs as papillae of columnar cells dispersed over an otherwise cuboidal epithelium. Depending upon the species, these papillae can produce a variety of hard structures: calcareous scales, spicules, or spines and/or chitinous hairs. Some papillae also produce bulbous outgrowths called nodules or "morgensternförmigen Körper" (morning star-shaped bodies). These nodules contain the dendrites of sensory neurons and are thought to be mechanoreceptive. Nodules can occur alone in the cuticle or in conjunction with calcareous spicules. Nodules of this type are present in the hairs of chitons in the genus *Mopalia.* Hairs from other mopaliid genera are also innervated, although they can lack these particular structures. In most species of chitons that I examined, nodules are made in conjunction with the ventral girdle spicules and the marginal spicules. These presumptive mechanoreceptors could be ubiquitous among chitons, as all species possess marginal spicules and overlapping ventral spicules. Hairs could have evolved to extend the reach of these tactile receptors beyond the surface of the animal's body, as well as to provide mechanical protection from desiccation and predation.

The external surfaces of the polyplacophoran girdle are armed with diverse types of secreted structures whose form and arrangement is species specific. These secretions include calcareous spicules, spines, and scales, and chitinous hairs (Fischer-Piette and Franc, 1960) (Figs. 1, 2). The dorsal surface can produce several types of hard parts, while the mantle edge and ventral surfaces generally produce one type of ornament each (Hyman, 1967). These structures can be completely or partially embedded in the cuticle that covers the epidermal cells of the girdle. These girdle formations, or ornaments, can be simple or composite structures (Fig. 1). Individual, fusiform, calcareous spicules are often totally embedded in the cuticle, which is 25 to 100 μm thick, whereas longer calcareous spines (Figs. 1, 2b) have only their proximal ends in the cuticular matrix (Plate, 1898, 1902; Hyman, 1967). Many species produce overlapping calcareous scales (Fig. 2a) that are also connected to the cuticle basally. Species in several families produce hairs (Fig. 2c), often called setae or bristles, that can be simple, jointed (articulated), or composite chitinous shafts that extend beyond the girdle surface. Hairs usually consist of an extension of the cuticular matrix and can be surrounded by a more densely staining cortex (Leise and Cloney, 1982).

Most spicules are surrounded by a layer or "cup" of material that is darker than the enveloping cuticular matrix and stains more densely in sectioned material (Figs. 1, 3) (Plate, 1898, 1902; Knorre, 1925; Leise and Cloney, 1982). In spicules from many species, this dense cup is elongated into a shaft that extends from the spicule to the epidermal cells (Fig. 1). The similarity of many hairs to this type of spicule shaft and the presence of a spicule at the distal tip of many hairs, led Thiele (1929) and Hyman (1967) to suggest that spicules and hairs represent the two ends of a continuum of girdle structures. They regard hairs as highly modified shafts of spicules. I continue their usage here and refer to hairs as those structures in which a chitinous shaft projects above the surface of the girdle and is the predominant part of the organ.

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[1] Present address: Otology Lab, 1159 Surge III, University of California, Davis, CA 95616.

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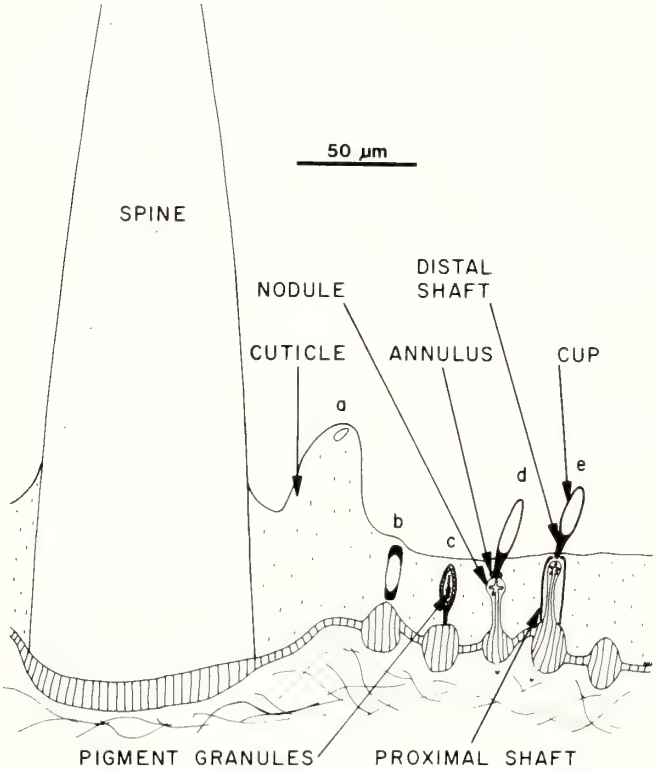


Fig. 1. Diagram of five types of spicules and one spine. **a.** Primary spicule from a newly metamorphosed juvenile. Note thin chitinous cup. **b.** Spicule with apically and basally thick cup. **c.** Spicule with pigment granules and shaft. **d.** Spicule with an annulate shaft surmounting a sensory nodule. **e.** Spicule as in d but with an articulated shaft (from Leise, 1983).

As will be described below, most hairs contain or are in contact with dendrites from presumptive sensory neurons. This paper reviews the morphology of chiton hairs while focusing on their neuronal elements and describes the relationships of these hairs to other girdle ornaments.

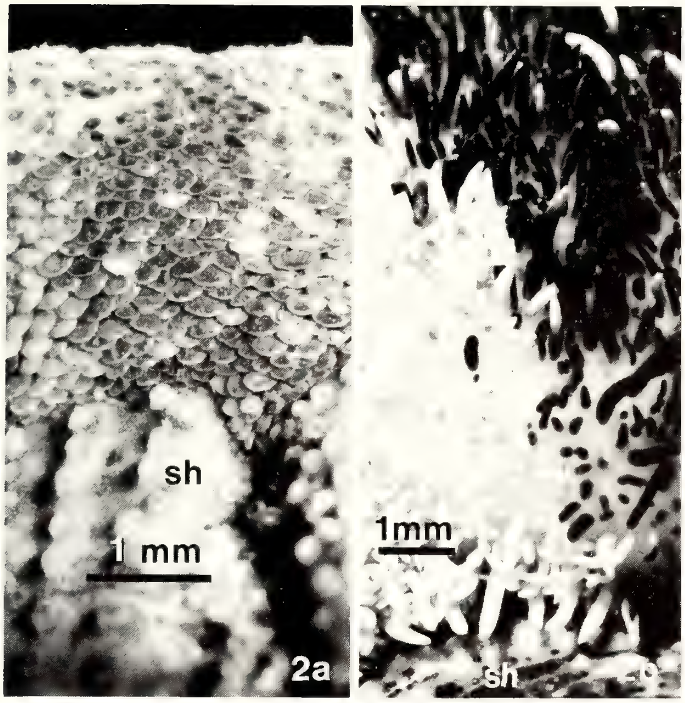
DIVERSE GIRDLE HAIRS: AN OVERVIEW

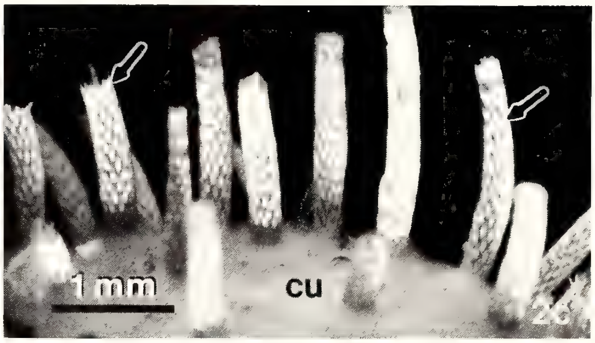
Hairs occur in a bewildering range of sizes and configurations in species from at least five families: Chitonidae; Lepidochitonidae (Ferreira, 1982); Callochitonidae; Chaetopleuridae; and Mopaliidae [classification after Bergenhayn (1955) unless otherwise cited]. In addition, hairs from many species of chitons will erode during the animal's lifetime. Thus, it can be difficult to understand the morphology of a particular type of hair if only large hairs or hairs from old animals are studied. Species such as *Chiton olivaceus* Spengler, 1797 (family Chitonidae) can produce small marginal hairs 80 to 100 µm long (Plate, 1902). In the Lepidochitonidae (Ferreira, 1982), species such as *Tonicella insignis* Reeve, 1847 produce small, simple hairs only 100 µm long (Leise, 1983), while others, such as *Dendrochiton lirulatus* Berry, 1963, produce tufts of hairs up to 500 µm long. Hairs from species of Callochitonidae, such as *Eudoxochiton nobilis* Gray, 1843, often have large articulated shafts about 1.5 mm in length (Leise, 1983). On intact animals of *E. nobilis*, even the distal spicules can be discerned. Species in the Chaetopleuridae and Mopaliidae also display hairs in a wide range of sizes; although the Chaetopleuridae characteristically produce hairs (Pilsbry, 1893), some species, like *Chaetopleura lurida* (Sowerby, 1832) secrete none. The girdle of this species bears spicules with articulated and simple shafts. A congener, *C. peruviani* Lamarck, produces similar spicules whose elongated shafts extend beyond the cuticular surface and so earn them the designation of hair (Plate, 1902; Fischer-Piette and Franc, 1960) (Fig. 4). Among the Mopaliidae are also species that produce small, simple hairs, such as those on *Katharina tunicata* Wood, 1815 or very large, simple hairs, as are found on *Plaxiphora obtecta* (Carpenter in Pilsbry, 1893) (Table 1).

Most of the above mentioned hairs conform to the hypothesis of Thiele (1929) and Hyman (1967) that hairs are elongated spicule shafts. However, the large hairs secreted by species in the genera *Mopalia* and *Placiphorella*, and those secreted by some of the Lepidochitonidae, namely *Lepidochitona flectens* (Carpenter, 1864), and species in the genus *Dendrochiton* Berry, 1911 (Ferreira, 1982), do not conform to Thiele's (1929) and Hyman's (1967) hypothesis. These latter types of hairs are composite structures, built by the replication of many basic units. They are not simply enlarged or elongated spicule shafts. In the genus *Mopalia*, the basic unit construct is a calcareous spicule and its long chitinous shaft. This basic unit is serially repeated along an outgrowth of the cuticle, and with the exception of the groove along which these spicules lie, the entire organ is surrounded by one or two distinct layers of dense cortical material (Fig. 5) (Leloup, 1942;

Table 1. Characteristics of chitons hairs in the family Mopaliidae (Structure: C = compound; S = simple and lacking medulla. Length and width are maxima recorded. Cortex: ++ = >20 µm thick; + = <20 µm thick; − = lacking).

Species	Hair Length (mm)	Hair Width (µm)	Structure	Cortex	Innervation
Mopalia muscosa	5	400	C	++	+
M. ciliata	3	200	C	++	+
M. lignosa	3	300	C	+	+
M. hindsii	2.5	80	C	+	+
Plaxiphora obtecta	2	300	S	++	−
Katharina tunicata	0.1	5	S	+	+
Placiphorella velata	5	400	C	−	+





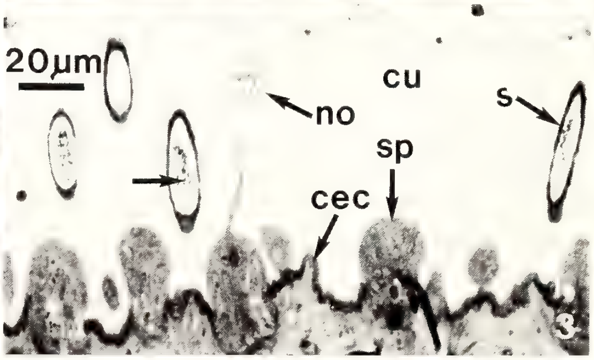


Fig. 2. a. Dorsal integument of *Lepidozona cooperi* (Pilsbry, 1892) demonstrating overlapping scales. **b.** Dorsal integument of *Acanthopleura granulata* (Gmelin, 1791) displaying calcareous spines. Cuticle is visible between spines. **c.** Dorsal hairs of *Placiphorella velata.* Numerous spicules (arrows) are embedded near the surface of each hair (cu, cuticle; sh, shell) (from Leise, 1983). **Fig. 3.** Transverse 1 μm section through the decalcified integument of *Mopalia muscosa.* Spicules (s) produced by spiniferous papillae (sp) contain brown pigment granules (arrow). One spiniferous papilla has produced a sensory nodule (no). Part of its stalk is not in the plane of this section. Common epidermal cells (cec) occur between papillae (from Leise and Cloney, 1982).

Leise and Cloney, 1982). Similarly, in the genus *Placiphorella*, the hair is an extension of the cuticle and is entirely covered with spicules that lie in whorls just below the surface of the hair (Fig. 2c) (Plate, 1902). From Ferreira's (1982) descriptions, the hairs of *L. flectens* and the genus *Dendrochiton* appear likewise to be branched or compound structures and not simply enlarged spicule shafts.

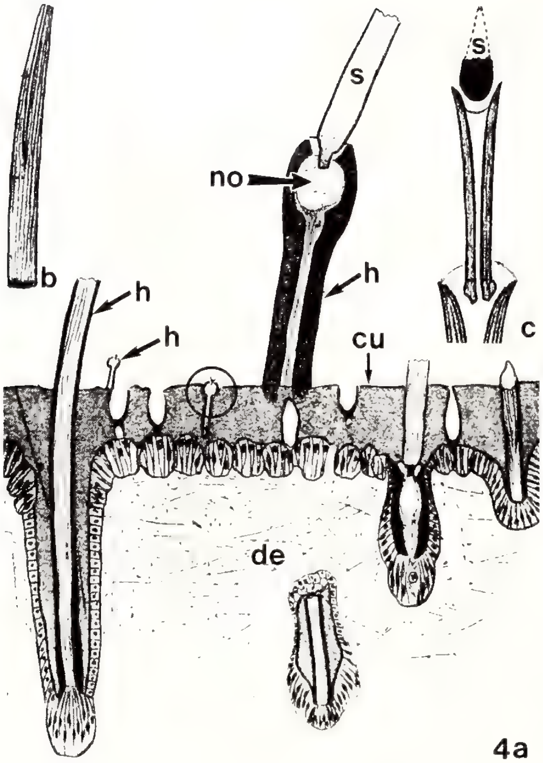
THE MORPHOLOGY OF HAIRS OF *MOPALIA MUSCOSA:* A MODEL FOR COMPOSITE SENSORY HAIRS

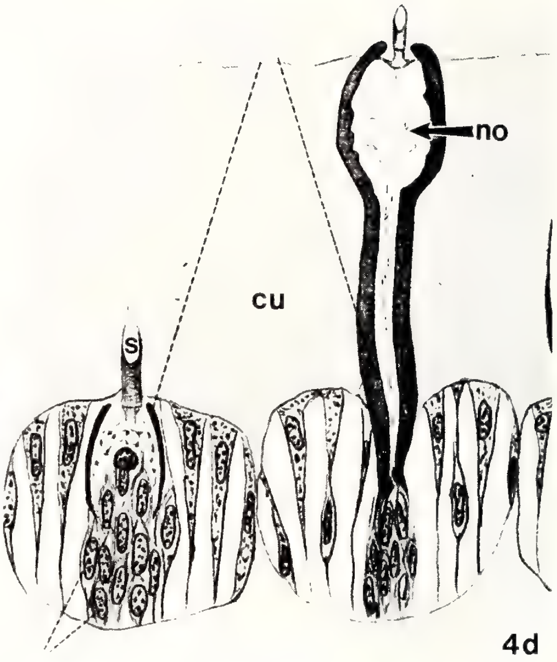
A fully-formed hair of *Mopalia muscosa* is a curved, distally tapered extension of the cuticle that bears a mesial groove in which lies a row of spicules (Figs. 5, 6). Each spicule occurs atop a distinct shaft, whose proximal end is embedded in the cuticular matrix, or medulla. The medulla is enveloped by a bilayered cortex, except for the mesial groove, and is therefore exposed to the environment along the length of that groove. Within the medulla, the proximal end of each spicule shaft surmounts a bulbous epidermal projection, a stalked nodule (Leise and Cloney, 1982) or "morgensternförmig Körper" (morning star-shaped body) (Reincke, 1868). Blumrich (1891), Knorre (1925), and Plate (1898, 1902) described such nodules in many species. All of these authors suggest that the nodules are tactile. Until recently (Leise and Cloney, 1982), their presence in hairs of the Mopaliidae was unknown.

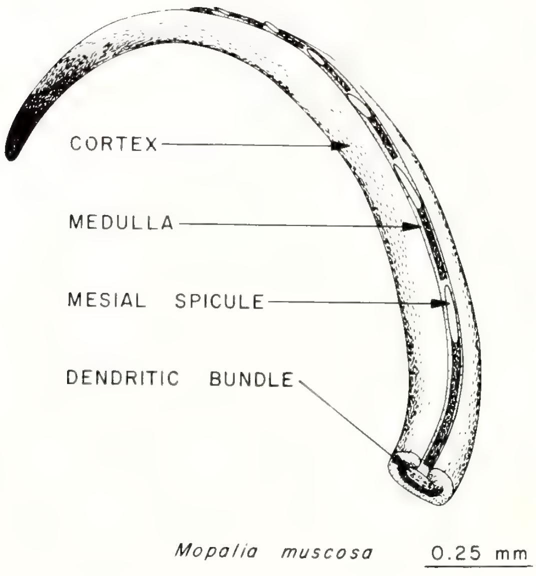
The dorsal girdle epidermis is a single layer of cells that is divided into numerous packets or papillae of columnar cells. These papillae produce the hairs, spicules, and nodules. Smaller cuboidal cells occur ubiquitously between the papillae. The papillae that produce the hairs are the largest in the epidermis and as a hair matures, the papilla comes to lie in a small depression or pocket below the level of the rest of the epidermal cells (Leise and Cloney, 1982; Leise, 1986).

Each subcortical cell produces a bundle of cortical fibers (Figs. 6, 7). The fiber bundles of the inner cortex are more dense than those of the outer cortex (Leise and Cloney, 1982). Each layer of the cortex in a mature hair is several bundles thick, whereas in young hairs the cortex is only one bundle wide. Newly forming hairs have no cortex and start as a single spicule with an elongated shaft that lies above a stalked nodule. More spicules and their associated shafts and nodules are added to the growing cuticular hair and only after several nodules are present does cortex begin to appear. The cortex is initially a narrow crescent along the lateral edge of the hair. As development proceeds, the hair grows longer and the cortex become progressively wider until it encompasses nearly the entire shaft (Leise, 1986).

Submedullary cells occur as a hillock that protrudes into the base of the hair shaft and presumably secrete the medullary matrix. The sensory cells lie in clusters within this







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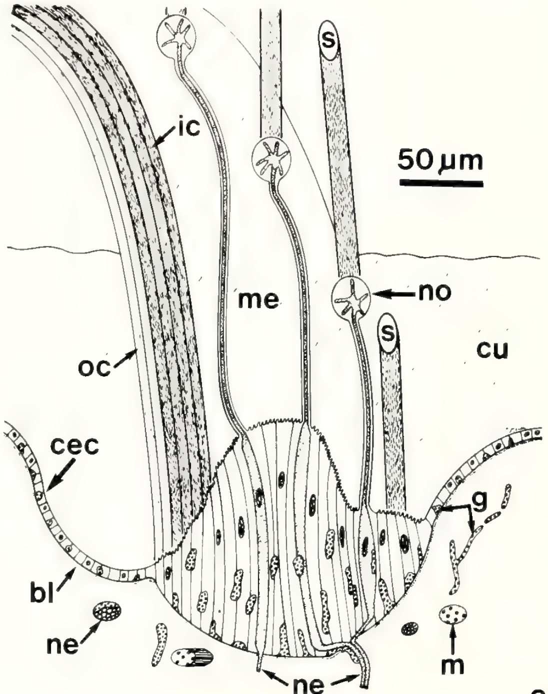

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Fig. 4. a-d. Diagram of spicules and hairs of *Chaetopleura peruviana.* **a.** Three hairs (h) occur above the cuticle (cu). All three hairs are simple; the right two are each capped by a spicule (s) and appear to contain stalked nodules (no). **b.** Tip of a simple hair. **c.** Tip of an articulated hair with distal spicule (s). **d.** Enlargement of the small spicule circled in a whose shaft contains a stalked nodule (no) (de, dermis) (from Plate, 1902). **Fig. 5.** Diagram of the external morphology of a hair of *Mopalia muscosa.* The base of the shaft of each mesial spicule is embedded in the medulla. Below each shaft is an epidermal sensory nodule. The cut ends of the nodule stalks are visible in the medulla. The hair is drawn in its entirety as if it were cut off just beyond the cuticle (from Leise, 1986). **Fig. 6.** Diagrammatic longitudinal section through the base of a hair of *Mopalia muscosa*, drawn passing through the mesial groove and two spicules (s). Dendrites from three sensory neurons terminate in nodules (no). In mature hairs, the sensory neurons occur in clusters, not as single cells, as they are drawn here, for clarity. Two nerves (ne) cross the basal lamina (bl) as they emerge from the base of the papilla (cec, common epidermal cells; cu, cuticle; g, pigmented glial cells; ic, inner cortex; m, muscle fiber; me, medulla; oc, outer cortex).

hillock and each cluster produces a long bundle of dendrites that extends through the hair (Figs. 6-9) (Leise and Cloney, 1982). The oldest dendritic bundle extends to the tip of the hair; younger bundles are progressively shorter. Each dendritic bundle ends in a nodule, just below the shaft of a mesial spicule (Fig. 6). A hair can have from one to 20 nodules in it, arising from the same number of neuronal clusters in the submedullary hillock (Leise and Cloney, 1982). One or several nerves emerge from the base of each trichogenous (hair-producing) papillae (Figs. 6, 7, 10). These nerves are presumed to contain the axons of the submedullary sensory neurons (Fig. 10). Although these basal axons have not been definitively shown to arise from the neurons (i.e. the submedullary neurons could be axonless, synapsing upon sensory interneurons from the CNS, or the submedullary "neurons" could have been misidentified and the nerves could have other functions) (see also following section), the most obvious explanation is that the epidermal cells whose long apical necks contain numerous parallel microtubules are primary sensory neurons (Leise and Cloney, 1982). Finally, there are usually fewer nerves than nodules within one papilla, indicating that the axons from several clusters of neurons converge onto a single nerve (Fig. 6).

Each nodule (and hence each dendritic bundle) contains dendrites from several cells, there being from one to 25 dendrites per bundle (Fig. 9) (Leise and Cloney, 1982). Each bundle is surrounded by one or two submedullary supporting cells. The dendrites often branch, so a tally of the number of dendrites in a bundle overestimates the number of sensory neurons. In figure 6 the sensory dendrites are drawn as straight cylinders with only one neuron per cluster for ease of presentation. Within the nodule, the dendrites ramify between the processes of the submedullary supporting cells that contain large vacuoles (Fig. 11).

SENSORY HAIRS FROM OTHER MOPALIIDAE

To gain some understanding of the occurrence of sensory hairs throughout the Mopaliidae, I examined the girdle integuments of six other species in this family. Animals were collected from rocky intertidal regions in Puget Sound, Washington, or on Vancouver Island, British Columbia (Leise, 1983). Samples of girdle integuments were fixed in Millonig's phosphate buffered glutaraldehyde and post-fixed in bicarbonate buffered osmium tetroxide (Cloney and Florey, 1968). Detailed procedures are described elsewhere (see Leise and Cloney, 1982; Leise, 1983). Specimens of *Plaxiphora obtecta* were obtained indirectly from New Zealand, where they were fixed in 5% formalin in seawater.

In addition to various shell and body characteristics, one of the mopaliid diagnostic features is the production of dorsal girdle hairs. From most accounts, the one exception in this hairy family appeared to be *Katharina tunicata*. However, Leloup (1940) noticed that the girdle of this species produces tiny translucent hairs (Table 1). I confirmed this observation and found that the papillae that secrete these hairs are also innervated (Fig. 12).

Three other species of *Mopalia*, namely *M. ciliata, M. hindsii,* and *M. lignosa,* have innervated hairs similar to those of *M. muscosa* (Fig. 13). Interspecific variation occurs in size, number of nodules per hair, extent of cortical envelopment, and size and arrangement of spicule shafts (Leise, 1983).

The hairs of *Placiphorella velata* Dall 1878 (Fig. 2c) are quite different from those in the genus *Mopalia*. *Placiphorella* hairs contain no nodules, although they are innervated (Plate, 1902; Leise, 1983). Instead of lying above a nodule, each spicule in these hairs lies above a cell that projects beyond the hillock on a thin stalk (Fig. 14). The ultrastructure of these cells deserves attention as they too are likely to be sensory neurons. As Plate (1902) reported for *P. stimpsoni* (Gould, 1859), several nerves emerge from the epidermis below each of the hairs of *P. velata*. Again, these nerves probably carry axons from the primary sensory neurons, and axons from many neurons converge into each nerve.

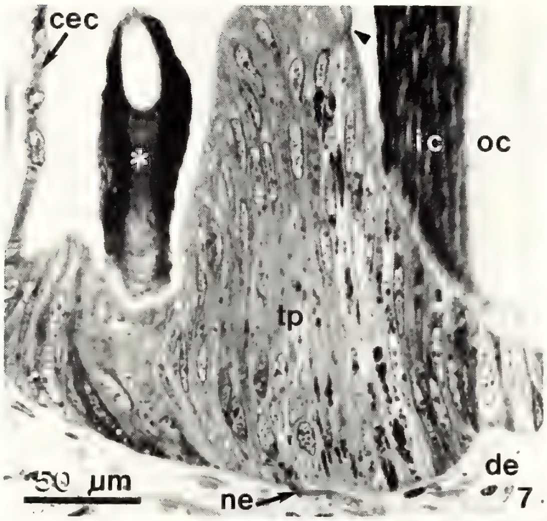
I also examined the hairs of *Plaxiphora obtecta*, which are large discrete shafts of cortical material (Fig. 15, Table 1). In sectioned material I found no nerves emerging from the bases of their trichogenous papillae. With this exception, all of the mopaliid hairs that I examined either contained or contacted epidermal neurons (Leise and Cloney, 1982; Leise, 1983). The hairs of *P. obtecta* could truly lack innervation, or this lack could be the result of inadequate fixation.

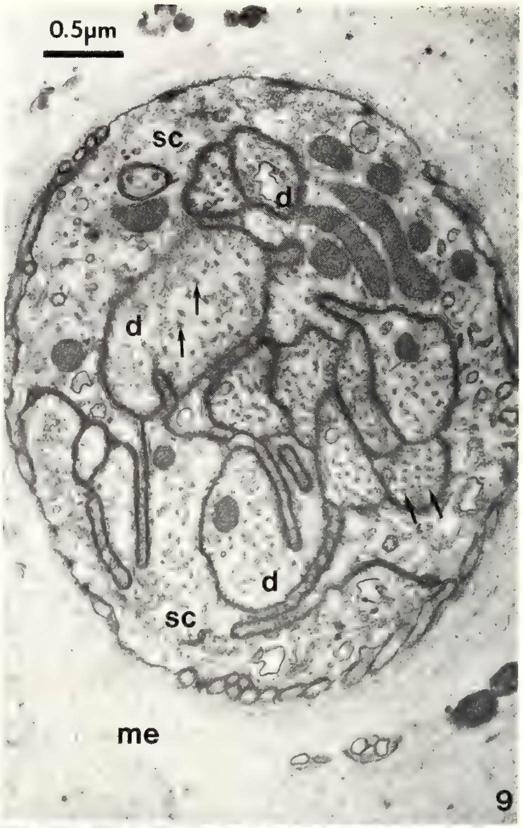
Stalked nodules, such as those in hairs of mopaliid genera, have been observed in the epidermis of many chitons (Fig. 3; Table 2) and repeatedly hypothesized to be tactile (Blumrich, 1891; Plate, 1898, 1902; Knorre, 1925; Thiele, 1929; Haas and Kriesten, 1975; Fischer *et al.*, 1980). However, the papillae that produce these nodules had not been shown to send nerves into the dermis until the work of Leise and Cloney (1982; Leise, 1983). All stalked nodules are not identical, as is discussed below. The functional distinctions between the various types of nodules are unknown.

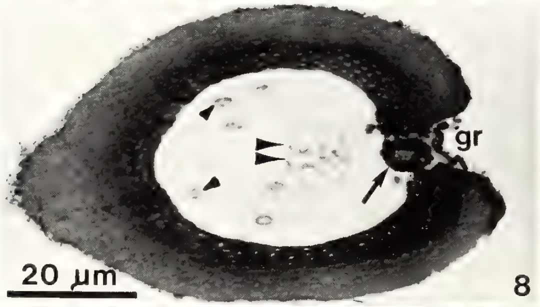
OCCURRENCE OF SENSORY NODULES IN THE CHITONS

According to Blumrich (1891), all chitons possess a fringe of spicules around the mantle edge. In many cases, the shafts of these marginal spicules contain or surmount a stalked nodule (Table 2) (Plate, 1898, 1902; Knorre, 1925). The hollow shafts of spicules in some species contain more claviform (club-shaped) cellular protrusions that lack a slender stalk (Blumrich, 1891; Plate, 1898, 1902; Knorre, 1925). I examined the ultrastructure of claviform nodules in *Katharina tunicata* and found that they too contain dendrites from epidermal sensory neurons and that the dendrites ramify between vacuolated processes of epidermal supporting cells. Other epidermal protruberances described by Fischer *et al.* (1980) resemble incipient stalked nodules of *Mopalia muscosa* (Leise, 1983). In this review I refer to all of these epidermal protrusions as stalked nodules.

Only on the dorsal surface of the girdle are stalked nodules reported to occur alone (Fig. 3) (Blumrich, 1891; Haas and Kriesten, 1975; Fischer *et al.*, 1980; Leise and Cloney,







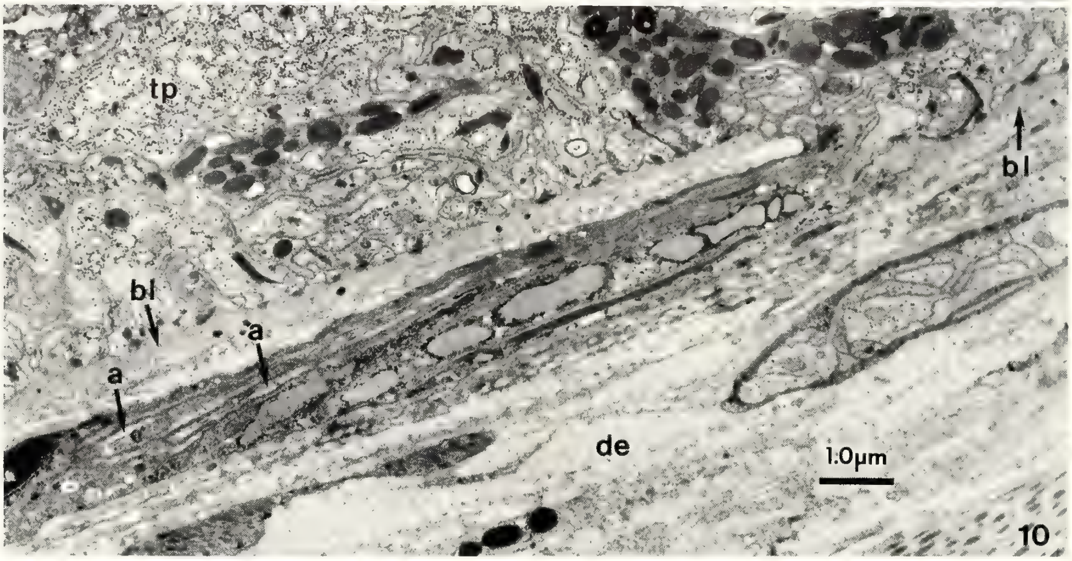


Fig. 7. Median longitudinal 1 µm section through the base of a girdle hair of *Mopalia muscosa*. Common epidermal cells (cec) line the pocket in which the trichogenous papilla (tp) lies. This section grazes the shaft (asterisk) of a mesial spicule (c.f. Fig. 6). The continuity of the medulla and cuticle is visible just above this shaft. The proximal end of the dendritic stalk of a sensory nodule is emerging from the papilla (arrowhead). One nerve (ne) emerges from the base of the papilla and enters the dermis (de) (ic, inner cortex; oc, outer cortex) (from Leise and Cloney, 1982). **Figs. 8.** Transverse 1 µm section through a hair of *Mopalia muscosa*, above the cuticle. Six dendritic bundles (arrowheads) and one nodule (double arrowheads) lie in the medulla. The groove (gr) in the cortex exposes the medullary matrix to the environment and is broader in younger hairs. The shaft (arrow) of the last mesial spicule lies just inside the groove (from Leise and Cloney, 1982). **Fig. 9.** Transverse section through the stalk of a sensory nodule from a hair of *Mopalia muscosa*. Numerous dendrites (d) are enclosed by two supporting cell (sc). The dendrites contain numerous parallel microtubules (arrows) and mitochondria (me, medulla). **Fig. 10.** Axons (a) emerge from the base of a trichogenous papilla (tp). The nerve passes into the dermis (de) from the base of the papilla. Note that the epidermal basal lamina (bl) does not surround the nerve.

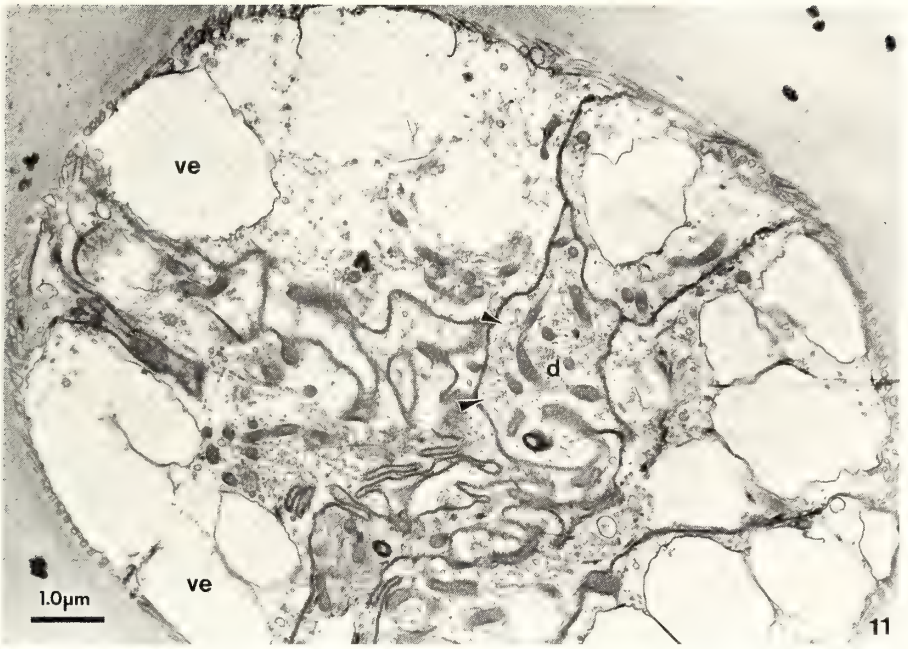


Fig. 11. Electron micrograph of a sensory nodule from a hair of *Mopalia muscosa*. In nodules, the dendrites (d) lose their typical organization; their mitochondria are twisted and the microtubules are no longer in parallel arrays (arrowheads). Large electron-lucent vacuoles (ve) lie around the periphery within the surrounding cells.

1982; Leise, 1986). In most cases, dorsal nodules are subjacent to spicules. The ventral girdle in all chitons produces overlapping spicules (Blumrich, 1891; Pilsbry, 1892, 1893; Knorre, 1925; Fischer-Piette and Franc, 1960; Hyman, 1967) and in many cases these spicules also contact sensory nodules (Table 2). Two exceptions are *Placiphorella velata* and *P. stimpsoni*, in which the ventral spicules contact stalked cells that are much like those in the dorsal hairs. These cells too will probably prove to be sensory neurons upon further study. Curiously, in *P. velata* the marginal spicules are associated with typical stalked nodules (Plate, 1902; Leise, 1983).

Of the chitons I studied, in only two species did I find claviform nodules without innervated papillae: *Eudoxochiton nobilis* and *Plaxiphora obtecta*. These animals were fixed in 5% formalin (see Leise, 1983) which does not preserve cellular ultrastructure as well as the combination of glutaraldehyde and osmium tetroxide. Thus, it is possible that the slender (1-2 μm in diameter) epidermal nerves were not preserved well enough for me to recognize them. It would be most surprising if these two species alone show no innervated epidermal sensory organs.

FUNCTIONS OF CHITON HAIRS

The functions of chiton hairs are not well understood although plausible hypotheses abound. Hyman (1967) describes chiton hairs as armature, although chitons bearing hairs are successfully preyed upon by starfish (Mauzey *et al.*, 1968; Paine, 1980), seagulls (Moore, 1975), fish (Ronald Shimek, pers. comm.) and humans. The girdle could be toxic or distasteful but it does not provide sufficient protection

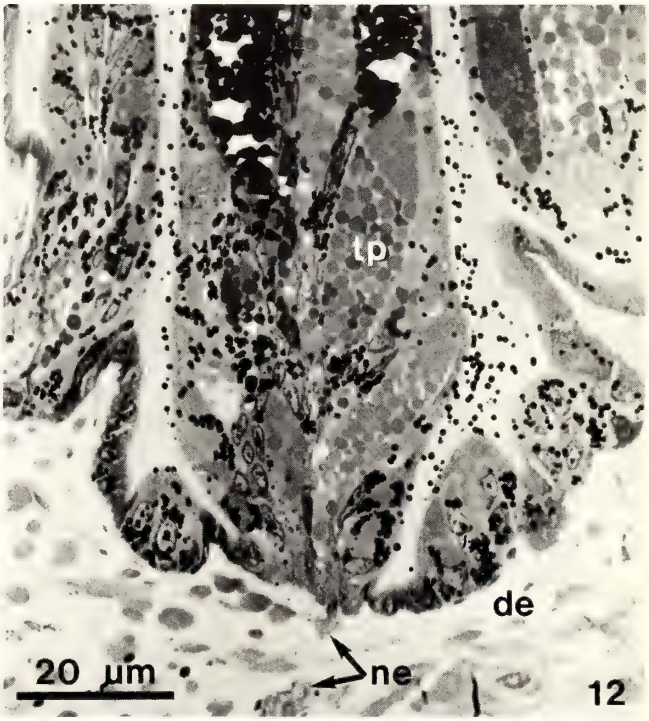


Fig. 12. Longitudinal 1 μm section through the base of a trichogenous papilla (tp) of *Katharina tunicata*. One nerve (ne) emerges from the base of the papilla then continues into the dermis (de) (from Leise, 1983). Many cells of these papillae also produce granules, which can be seen here in their various stages of condensation. Eventually, granules are extruded into the cuticle.

Table 2. Location of sensory nodules in or in conjunction with the designated girdle ornament. Alone indicates in cuticle without attached spicules or hairs [* = animals I examined. Superscripts 1, 2, and 3 designate information from Plate (1898, 1902); Knorre (1925) and Fischer *et al.*, (1980), respectively. NA = not applicable].

Family and Species	Alone	Dorsal Spicules	Marginal Spicules	Ventral Spicules	Dorsal Spicules
Lepidopleuridae					
Lepidopleurus cajetanus^1		+			
Ischnochitonidae					
Ischnochiton herdmani^2	–	+	+		NA
*Lepidozona retiporosus**	–	–	+	+	NA
Lepidochitonidae					
*Lepidochitona dentiens**	+	–		+	NA
L. cinerea^2	+	+			NA
*Tonicella insignis**	–	–			+
Callochitondae					
*Eudoxochiton nobilis**	–	–			–
Chaetopleuridae					
Chaetopleura peruviana^1	–	–			+
*C. lurida**	–	+	+	+	NA
Mopaliidae					
*Plaxiphora obtecta**	–	–	–	–	–
Katharina tunicata–	–	NA		+	–
*Katharina tunicata**	+	–	+	+	+
*Mopalia ciliata**	+	–			+
*M. lignosa**	+	–	+	+	+
*M. muscosa**	+	–	+	+	+
*Placiphorella velata**	–	–	+	–	–
Chitonidae					
Chiton olivaceus^1	–	NA	+	+	
Acanthochitonidae					
Acanthochiton fascicularis^3	–	+	–	+	NA

against predation. Predators tend to eat the foot and viscera, discarding the shell and girdle.

Species with large and abundant hairs such as *Mopalia muscosa* often support extensive epiphytic and epifaunal communities (Phillips, 1972). This covering retains water and could protect the animal against desiccation at low tides. This covering could also provide an additional defense against predation. *Pisaster ochraceus* (Brandt, 1835) will feed on *M. muscosa*, but if the chiton is covered with its normal detrital cloak, the starfish may fail to recognize it. After it touches an overgrown chiton, a starfish will ignore it. The basis for this protection, that is, whether the starfish's olfactory or tactile senses are deceived, is unknown. If the starfish contacts the girdle of a clean chiton, it detects a prey item and removes the chiton from the substratum. A chiton cannot escape a hungry starfish nor maintain a sufficiently strong grip on the substratum to avoid being consumed (pers. obs.). A chiton's epiphytic cloak could also afford protection from visual predators. Chitons with well developed epiphytic communities often resemble clumps of algae. Even during high tides, while they are moving and feeding, their identity could be concealed, as their slow rate of motion does not reveal their animal nature.

In addition to providing passive defenses, chiton hairs also mediate active responses from the animal. Chitons whose hairs are bent or pinched will turn away from the source of stimulation, or after several stimuli, tighten their grip on the substratum and remain motionless. This response appears to habituate rapidly, as prolonged or repeated stimulation will soon fail to invoke a response (Leise, 1983).

This tactile aspect of hair function could be most important to juveniles. In *Mopalis muscosa*, hairs first appear at metamorphosis (Leise, 1984) and although they do not initially display all of the adult characteristics, the first sensory neurons have differentiated and are presumably operational (Leise, 1986). These young animals take refuge in cracks and crevices in the substratum and their hairs may be important detectors of irregular surface features. Similarly, ventral nodules, which are widespread among the chitons, would give an animal feedback on the surface characteristics of its substratum and allow it to modulate its grip.

Although chiton hairs respond to touch, mechanoreception may not be their primary function. For example, they could be chemoreceptive. However, unlike other molluscan chemoreceptors (Laverack, 1968), the dendrites in the stalked nodules are embedded in the cuticle. I found no pores in the cuticle as exist in insect chemoreceptive hairs (Laverack, 1968). I was also unable to elicit any response from *Mopalia muscosa* upon application to the hairs (without moving the hairs) of various algae or tube feet from a predator starfish, *Pisaster ochraceus.*

As previously stated, a sensory function is the most

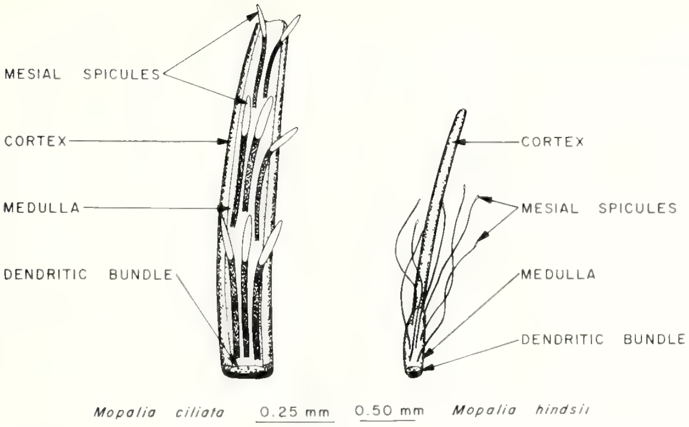
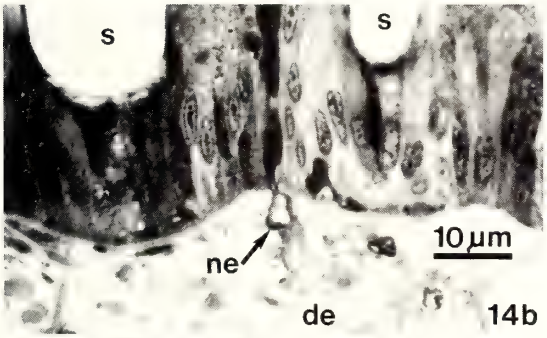

MESIAL SPICULES
CORTEX
MEDULLA
DENDRITIC BUNDLE
Mopalia ciliata
0.25 mm
0.50 mm
Mopalia hindsii
CORTEX
MESIAL SPICULES
MEDULLA
DENDRITIC BUNDLE
MESIAL SPICULES
CORTEX
MEDULLA
DENDRITIC BUNDLE
Mopalia lignosa
0.25 mm

Fig. 13. Diagrams of the external morphology of hairs from three species of *Mopalia.* Note that the cortex does not enclose the medulla in hairs of *M. hindsii* (from Leise, 1983).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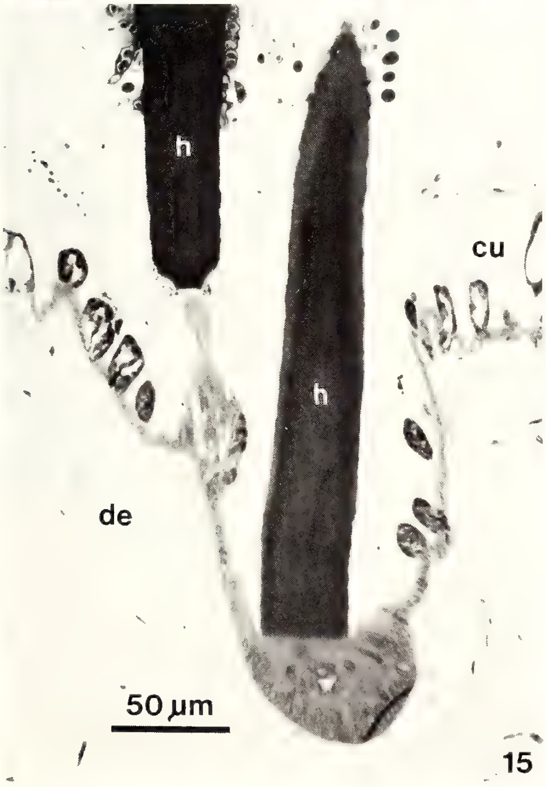
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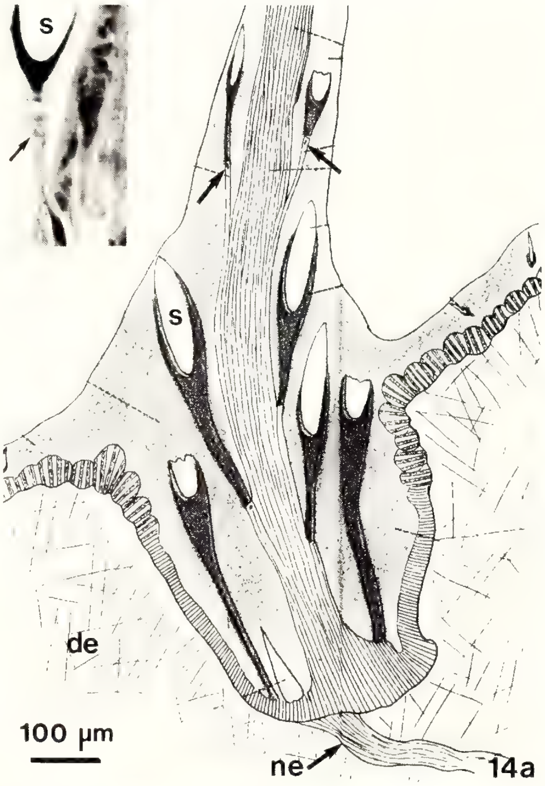
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Fig. 14. a. Diagram of a hair of *Placiphorella stimpsoni* (from Plate, 1902). Note spicules (s) atop individual cells (arrows) beyond the hillock of submedullary cells. One nerve (ne) emerges basally. Inset: micrograph of a similar spicule and its subjacent cell from a hair of *P. velata.* **b.** Longitudinal 1 μm section through the base of a partially decalcified trichogenous papilla of *P. velata* showing a nerve (ne) emerging at the base (de, dermis) (from Leise, 1983). **Fig. 15.** Longitudinal 1 μm section through two dorsal hairs (h) of *Plaxiphora obtecta* in one epidermal invagination. The right hair shaft is still being formed, while the extrusion of the left hair has ceased. Its papilla has produced a claviform cellular protrusion below the shaft. No nerves have been found to emerge from these papillae (cu, cuticle; de, dermis) (from Leise, 1983).

parsimonious explanation for the presence of an innvervated integument and cells that resemble sensory neurons. However, this explanation does not exclude the possibility that the basal nerves mediate other functions, such as contraction or secretion. I found no obvious contractile elements in the epidermis of *Mopalis muscosa*, although its skin does secrete the cuticle and ornaments. Epidermal cells in other species such as *Katharina tunicata* extrude pigment granules into the cuticle (Fig. 12) (Leise, 1983). Whether or not the nerves carry axons from neurons mediating epidermal secretion is unknown.

CONCLUSIONS

My results lead me to suggest that most chiton hairs are mechanoreceptors, although hairs are not the only girdle sensory organ. Stalked nodules occur far more widely than hairs, on the marginal and ventral surfaces of what may be a majority of the chitons (Table 2). These nodules are probably important sources of feedback to the animal about the nature of the surface on which it lives. Fischer *et al.* (1980) have also recognized photoreceptors in the girdle of *Acanthochiton fascicularis* that could in part be responsible for this chiton's response to changes in light intensity. Unfortunately, the existence of these girdle sensory organs is not widely recognized.

In her review of the functional morphology of the chiton epidermis, Hyman (1967) did not assimilate Plate's (1902) information about the sensory nature of girdle hairs nor the sentiment from the German literature that stalked nodules are tactile (Blumrich, 1891; Plate, 1898; Knorre, 1925; Thiele, 1929). Since then, the sensory nature of girdle structures has been studied or remarked upon by several authors (Beedham and Trueman, 1967; Haas and Kriesten, 1975; Fischer *et al.*, 1980). Most invertebrate texts include descriptions of chiton sensory organs in the mouth, on the subradular organ, in the buccal cavity, in the pallial grooves, and in the shell plates, but not in the girdle (Hyman, 1967; Meglitch, 1971; Gardiner, 1972; Barnes, 1987; Pearse *et al.*, 1987).

In *Mopalia muscosa*, hairs erode and lose spicules throughout the animals's life. As many species produce hairs and do so constantly during their lifetimes, the benefits from their presence must outweigh their productive costs. Hairs appear to have evolved several times in this class, as large hairs occur in diverse families and can be formed in several ways. Evolutionarily, there appear to be trends towards an increase in the size of girdle ornaments (Pilsbry, 1892; Leise, 1983) and towards an inclusion of sensory organs in these ornaments. Hairs are thus considered to be phylogenetically advanced features, as they also occur in stratigraphically newer families (Smith, 1960) and appear late in an animal's development.

The integument of most molluscs is richly endowed with sensory organs and individual sensory neurons that serve many modalities, including mechanoreception, chemoreception, and photoreception (Laverack, 1968). For the chitons to be "blind" to environmental stimuli over a large portion of their skin would indeed be surprising (Beedham and Trueman, 1967). The work of many authors reviewed here suggests that this is certainly not the case and that the girdle ornaments are not just passive armature but active participants in the lives of these animals.

ACKNOWLEDGMENTS

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THE ULTRASTRUCTURE OF THE AESTHETES IN *LEPIDOPLEURUS CAJETANUS* (POLYPLACOPHORA: LEPIDOPLEURINA)

FRANZ PETER FISCHER
INSTITUT FÜR ZOOLOGIE, TECHNISCHE UNIVERSITÄT MÜNCHEN
LICHTENBERGSTRASSE 4, D 8046 GARCHING,
FEDERAL REPUBLIC OF GERMANY

ABSTRACT

The aesthetes of *Lepidopleurus cajetanus* Poli consist of five different cell types: one or two photoreceptor cells are present in the periphery in many of these organs. Products of tall secretory cells pass through a perforated apical cap to the outside. Central cells probably are chemoreceptors. Micraesthete cells form lateral branches from the main stem and end with unperforated caps at the shell surface; their function is unknown. Peripheral cells form most of the border to the calcareous shell substance. It is proposed that this is the general composition of the aesthetes in chitons.

Aesthetes are numerous organs in the upper shell layer of the Polyplacophora (Figs. 1, 2). In recent years their fine structure has been studied in several species. Except for the species *Acanthochitona fascicularis* L. (Acanthochitonina) (Fischer, 1979), only members of the Chitonina have so far been examined in this respect (Boyle, 1974; Haas and Kriesten, 1978; Fischer and Renner, 1978; Baxter *et al.*, 1987). For the discussion on the function of these unique organs it is important to know which features are constant in the aesthetes and which are species-specific variations. In the present paper the aesthetes of a member of the relatively primitive suborder Lepidopleurina are described and their possible functions are discussed.

MATERIAL AND METHODS

Adult polyplacophorans of the species *Lepidopleurus cajetanus* Poli were collected in the subtidal (about 1 m below low tide level) region on the coast of northern Yugoslavia. Parts of the tegmental shell layer containing the aesthetes were removed and fixed in 5% glutaraldehyde in phosphate buffer (pH 7.4) for two hours and postfixed in 2% osmium tetroxide for two hours, all at 3°C. After dehydration in ethanol and propylene oxide the specimens were embedded in Durcupan. Some of the specimens were decalcified overnight in chilled 3% EDTA in phosphate buffer after glutaraldehyde fixation. The others were split into two pieces and the calcareous parts were removed by use of 5% HCl after embedding. Since the tissue is already penetrated by the embedding material, no damage occurred to the cells during this procedure, following which the specimens again were embedded in Durcupan to fill the holes left by the calcareous parts. Ultrathin sections were cut with a LKB or a Reichert ultramicrotome, stained with uranyl acetate and lead citrate (Reynolds, 1963) and studied in a Zeiss or a Jeol electron microscope.

For scanning electron microscopy, the organic material in the shell valves was removed by the use of concentrated KOH at room temperature for about one hour, cleaned in an ultrasonic cleaner and air dried. Other shells were air dried without previous treatment. The specimens were given a 300 Å thick coating with gold and were examined in a Cambridge SEM.

RESULTS

SHELL SURFACE

The head valve has the shape of a half circle with a few concentric ribs on the surface. In contrast, the other seven valves show two different surface areas (Fig. 3): the lateral fields resemble the head valve; parallel ribs are oriented along the long axis of the animal in the second to the seventh valve and are semicircular in the last one. In the median area of the valves II-VIII, 60 μm-wide elevations form rows that run mainly in the long axis. Parts of the articulamentum, the apophyses, protrude anteriorly to form a joint with the valve in front.

On the top of the elevations, as well as on the ribs, the openings of the aesthetes can be seen (Fig. 4), with a megapore (diameter= 11-14 μm) in the center, surrounded by 4-9 micropores (diameter= 9 μm). On the lateral areas, there are more micropores per megapore than in the median fields. The same is true for the absolute number of the aesthetes

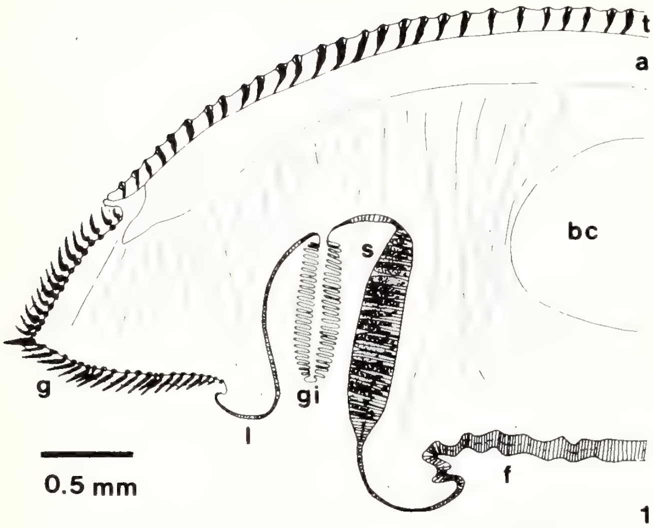

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Fig. 1. Schematic cross section through an adult *Lepidopleurus cajetanus,* left half (a, articulamentum; bc, body cavity; f, foot; g, girdle covered with spicules; gi, gill; l, lateral fold; s, secretory cells of the foot epithelium in the pallial groove; t, tegmentum with numerous incorporated aesthetes) (adapted from Maile, 1981).

(number of megapores), with about 150 per mm^2 in the lateral and 90 per mm^2 in the median area. The head valve has the highest density of aesthetes, about 200 per mm^2.

In untreated shell valves, each megapore is filled with the apical cap of the main stem (= megalaesthete) of an aesthete (Fig. 2). Each micropore contains the subsidiary cap of a micraesthete, which is a branch from the megalaesthete. In older aesthetes, the apical caps show a perforation with many pores of about 0.1 μm in diameter (Fig. 5). The subsidiary caps do not exhibit such a pattern. In young aesthetes the apical cap is completely covered by the periostracum.

AESTHETES

The aesthetes are, like the papillae in the girdle, extensions of the epidermis. Most of the cells of the aesthete are still connected with the epithelium via the aesthete canal. Some of these basal cell extensions are nervous elements and run further to the lateral nerve cords.

Each aesthete is about 110 μm long and 30 μm thick. It contains 35 to 40 cells of five distinct cell types: secretory cells, central cells, photoreceptor cells, micraesthete cells branching from the main stem, and peripheral cells (Fig. 2). Except for the micraesthetes, every type can exhibit a basal extension to the epithelium (Fischer, 1978a); for the micraesthete cells the situation is not yet clear. At the shell surface the main stem is covered by the apical cap and each micraesthete by a subsidiary cap.

APICAL CAP. The apical cap consists only of organic material and can be divided into two zones (Fig. 2): the distal part, containing numerous parallel pores and the proximal part, consisting of a network of thin filaments of two types. There are filaments of about 80 nm in diameter, which form the skeleton, from which 25 nm wide filaments branch off (Fig. 6). These fine filaments form the border of the cap to the interior of the aesthete.

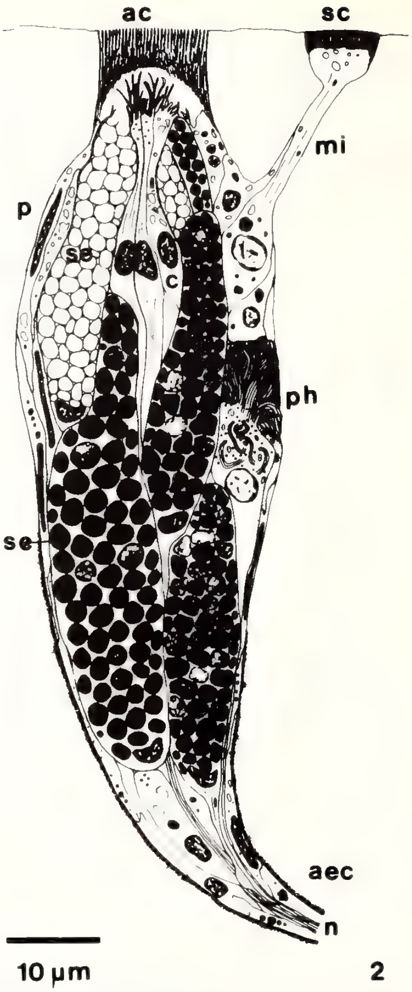

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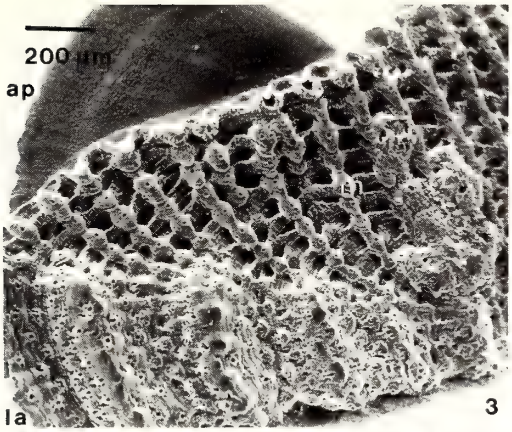
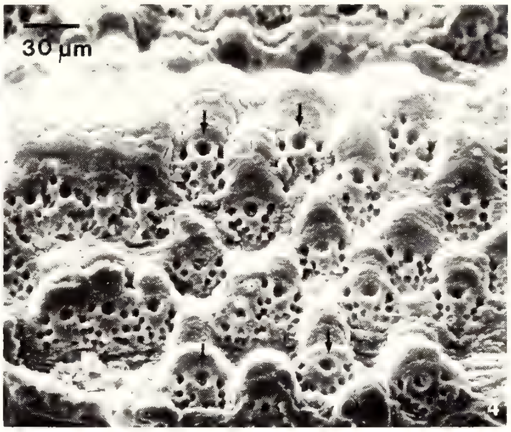
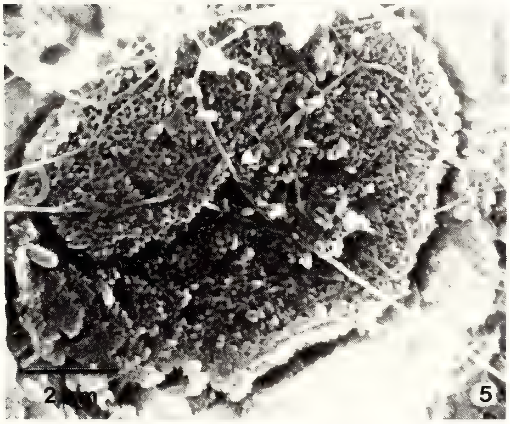
Fig. 2. Schematic longitudinal section through an aesthete (ac, apical cap; aec, aesthete canal; c, central cell; mi, micraesthete; n, neurites; p, peripheral cell; ph, photoreceptor cell; sc, subsidiary cap; se, secretory cell).

SECRETORY CELLS. Each aesthete has three to eight tall secretory cells of different forms. Some of them, especially in young aesthetes, show a high metabolic activity in the proximal part; granular endoplasmic reticulum (ER), a few Golgi apparatus and numerous mitochondria surround an active nucleus. The secretory granules produced are stored distally. Most of the secretory cells are densely filled with membrane bound secretion granules of various electron densities (Fig. 7). The nucleus lies basally, its chromatin is highly condensed (Fig. 8). Remains of endoplasmic reticulum and a few mitochrondria are often present nearby. One or two secretory cells that open distally secrete material beneath the apical cap. Some cytoplasm between the former granules remains; the interior is now continuous with the extracellular space beneath the apical cap (Fig. 9). In the neighbourhood of these







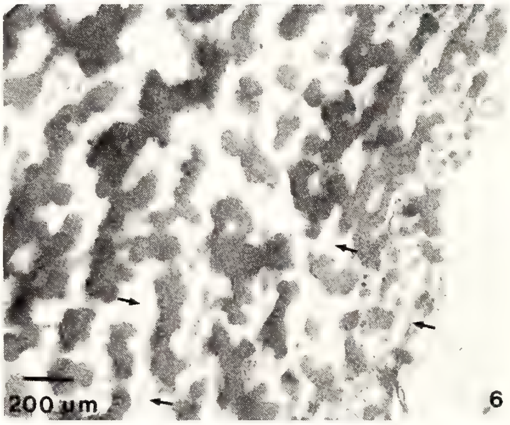


Fig. 3. Left half of an intermediate shell valve. KOH-treated (ap, apophyse; la, lateral triangle; m, median triangle). **Fig. 4.** Higher magnification of the lateral triangle, KOH-treated (arrows indicate several smaller micropores surrounding a megapore). **Fig. 5.** Surface of an apical cap. The cap is perforated by numerous small pores. **Fig. 6.** Longitudinal section of the basal area of an apical cap consisting of a network of larger and smaller (arrows) organic filaments.

cells, some of the peripheral cells exhibit characteristics of decomposing cytoplasm; lysosomes and autophagous vacuoles surround an active nucleus.

CENTRAL CELLS. The central cells (''sensory cells'' according to Boyle, 1974) (as the photoreceptor cell is also sensory, I use the more neutral term ''central cell'') of *Lepidopleurus cajetanus* are prominent compared with the other species studied so far. The nuclei of all central cells (about five per aesthete) are situated in the distal part of the aesthete. Distally, underneath the apical cap, each central cell forms numerous microvilli and one cilium (9+2 structure) (Fig. 10). The cytoplasm of the central cells contains numerous mitochondria and microtubules running along the long axis of the cells. Distally the cytoplasm is filled with clear 0.3 μm wide vesicles. The central cells are connected together by zonulae adhaerens and septate junctions.

PHOTORECEPTOR CELLS. Most of the aesthetes (but not all of them, irrespective of the position in different valve areas) contain one or two photoreceptor cells. They lie peripherally in the aesthete and do not exhibit a special orientation pattern, such as being always located on the same side of the aesthete body, as it is the case in *Chiton olivaceus* Spengler (Fischer and Renner, 1978). As in other species, they show two distinct areas, the cell body and the rhabdomere (Fig. 11). The microvilli (0.05-0.1 μm in diameter) of the rhabdomere branch from the whole distal part of the cell; they have no regular orientation. Their cytoplasm contains small granules. One or two cilia (9+2 structure) can be present.

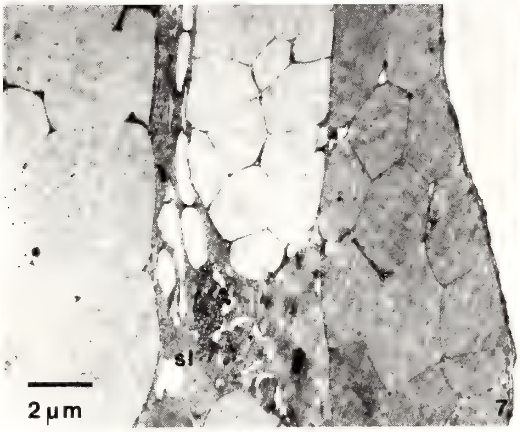
The nucleus is relatively large (6.5 μm) and has only a little condensed chromatin. In the perikaryon, numerous mitochondria, microtubules, glycogen and multivesicular bodies are present. A specialized agranular ER forms large areas of parallel membrane cisternae that are connected with the granular ER. Laterally these cisternae give off numerous clear vesicles (40-170 nm) that are found up to the rhabdome.

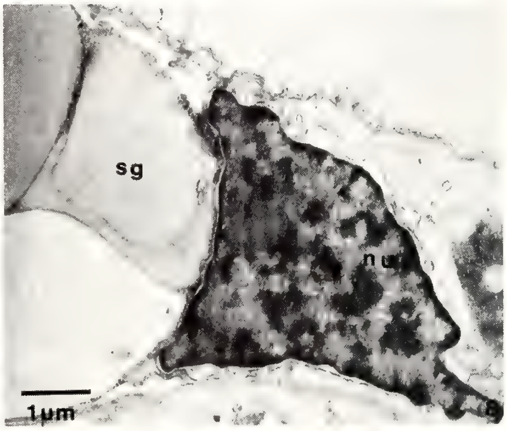
MICRAESTHETES. All micraesthetes branch off from the same zone of the main stem. Their nuclei lie in this area; they are large (6 μm) and have only little condensed chromatin. Here and in the ''arm'' (the part between the main stem of the aesthete and the tip of the micraesthete cell) we find numerous mitochondria and microtubules along the long axis (Fig. 12). In the basal part, multivesicular bodies or lysosomes are frequently found. Peripheral cells surround the proximal part of the "arm"; both cells show invaginations into the other cells. The "head" (the tip of the micraesthete cell) is slightly swollen and also contains mitochondria. The distal part forms numerous microvilli towards the subsidiary cap (Fig. 13). The "head" can show a high degree of vacuolization in some micraesthetes, but this zone does not continue into the "arm".

SUBSIDIARY CAP. In contrast to the apical cap, the subsidiary caps appear continuous at their outer and inner surfaces. They also consist of organic material. They contain inner pores (width= 0.1 µm), but in nearly all cases they are closed to the outside, as well as to the interior of the micraesthete, by continuous sheets. The distal sheet is up to 0.2 µm, the proximal sheet about 0.1 µm wide.

In some cases the micraesthete cap has been damaged by organisms. In these cases, parallel sheets of varying thickness are placed underneath the remainder of the cap. Sometimes, the subsidiary cap is completely replaced by this structure.

PERIPHERAL CELLS. The peripheral cells surround the





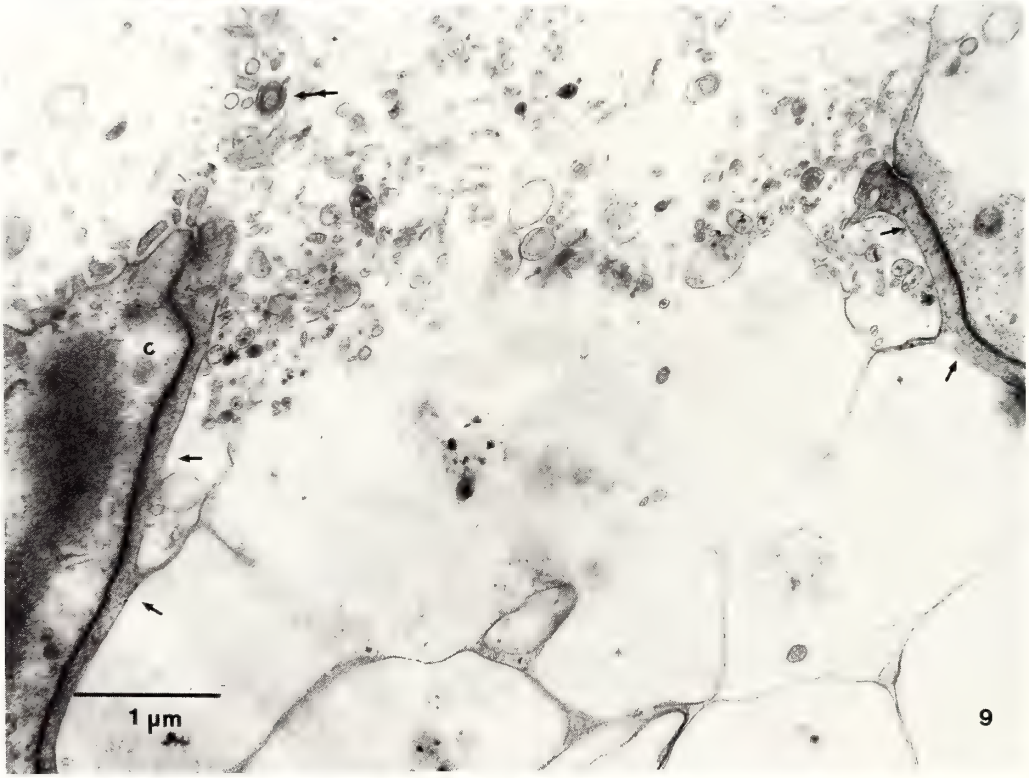


Fig. 7. Longitudinal section of an aesthete nearly completely filled with the granules of secretory cells (sl, secondary lysosome). **Fig. 8.** Base of a secretory cell (nu, highly condensed nucleus; sg, secretion granule). **Fig. 9.** Distal tip of a secretory cell after secretion. Surrounding cytoplasm (arrows) and small cytoplasmic remains are visible between the former secretion granules. The interior is now continuous with the extracellular material underneath the apical cap, in which microvilli and cilia (double arrow) of central cells are embedded (c, central cell).

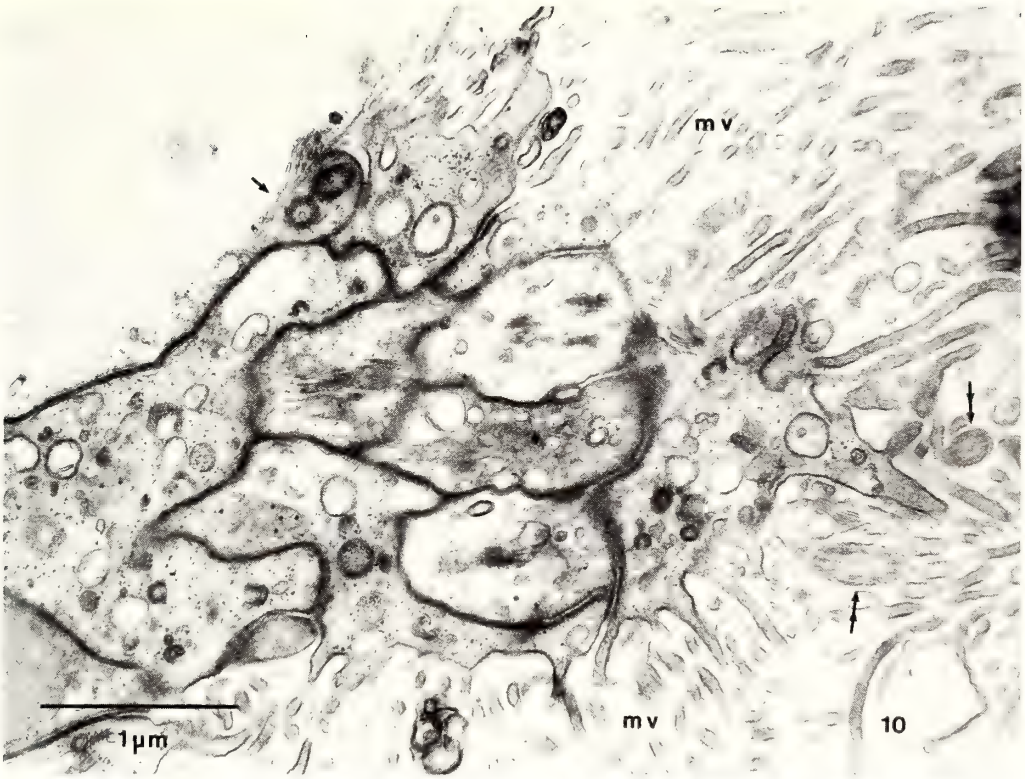


Fig. 10. Distal tip of central cells with protruding microvilli (mv) and cilia (double arrow). Arrow indicates basal body in a central cell.

body of the aesthete as a sheet about 0.75 μm in width. They are not present in all parts of an aesthete (e.g. Fig. 7). The fine structure varies considerably, e.g. in the content of decomposing structures. In the basal part of the aesthete, peripheral cells form an extracellular sheet of fine filaments into the shell material. Some of the filaments protrude, roughly perpendicularly, far into the shell substance.

AESTHETE CANAL. The aesthete canal is surrounded by peripheral cells (Fig. 14). In the center, various fibers (basal extensions of the aesthete cells to the epithelium) run towards the epithelium under or lateral to the shell valves. Some of the fibers connect the secretory cells with the epithelium; these fibers contain mitochondria and microtubules. About ten of the fibers are much thinner than those of the secretory cells (0.4 versus 1.5 μm). They are densely filled with microtubules and are probably nervous elements (Fig. 14). Structures resembling neurosecretory elements are also a regular feature in this area.

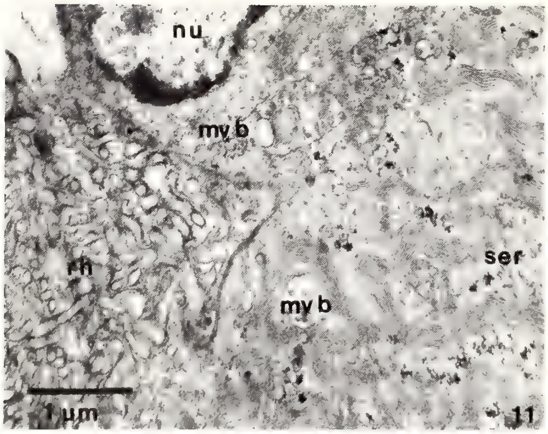
DISCUSSION

The general structure of the aesthetes of *Lepidopleurus cajetanus* is very similar to that of previously studied species. Despite the differences in the architecture of the shell valves, there is no major difference between the aesthetes in all three extant polyplacophoran suborders. The aesthetes are obviously an evolutionarily old system in the chitons.

The different cell types, each with pronounced ultrastructural characteristics, suggest that the aesthetes are compound organs with both a sensory and a secretory function. It is not clear whether some or all cell types work together to perform a more complex function or whether they function more or less independently.

The secretory cells produce secretions basally and release them apically. In *Chiton olivaceus*, animals outside the water show an increased secretory activity (Fischer, 1978a). Additionally, recordings with a glass microelectrode show slow rhythmic changes in the electrical potential under the same conditions (Fischer, unpub. data). This could suggest that one function of the secretion is to prevent the desiccation of the aesthetes during low tide. However, species that prefer to live in deeper water also have well developed secretory cells (Baxter *et al.*, 1987). The secretions probably have other protective functions, e.g. against predators or organisms growing on the shell. One indication for such a function is that the pores of the apical cap open only in older aesthetes, whereas newly formed aesthetes are covered by the periostracum.

The role of the central cells is not known. In their fine structure they resemble chemoreceptors of insects (Ernst, 1969). The position of this cell type underneath the perforated apical cap, the pronounced membrane proliferations (microvilli and cilia), and the high metabolic activity support such a hypothesis. Structures resembling nervous elements were



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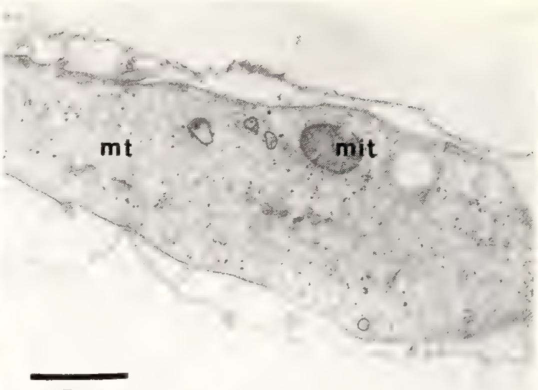

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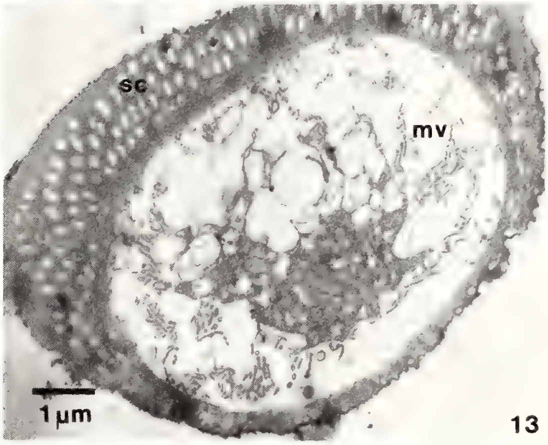

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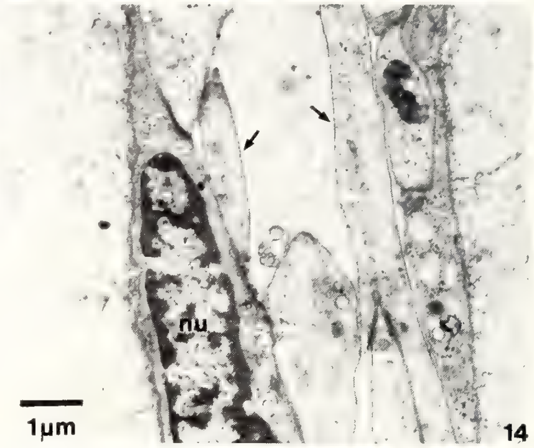

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Fig. 11. Photoreceptor cell at the transition of perikaryon and rhabdomere (mvb, multivesicular body; nu, nucleus; rh, rhabdomere; ser, specialised agranular ER). **Fig. 12.** Longitudinal section of the "arm" part of a micraesthete cell (mit, mitochondrion; mt, microtubules). **Fig. 13.** Subsidiary cap (sc) with the microvilli (mv) of the underlying micraesthete cell. **Fig. 14.** Longitudinal section through an aesthete canal (nu, nucleus of a peripheral cell). Arrows indicate profiles resembling neurites.

found near the base, but their relationship to the central cells is not clear. A possible function could be to detect desiccation and/or animals grazing on the shell (and eating also the distal parts of the aesthetes), with a subsequent reaction of the secretory cells. *Lepidopleurus cajetanus* has the best developed central cells of all species studied so far; in the Lepidopleurina the articulamentum is lacking in broad shell areas and the aesthetes are connected directly with the dorsal epithelium. Destruction of the aesthetes and a subsequent invasion of microorganisms into empty aesthete canals could be much more severe in this group than in the Ischnochitonina or the Acanthochitonina.

The photoreceptor cells resemble in detail the photoreceptor cells of *Chiton olivaceus* and *Acanthochitona fascicularis* (Fischer, 1978b, 1979; Fischer and Renner, 1978) as well as the photoreceptor cells in the two different shell-eye types in the chitons (Boyle, 1969; Haas and Kriesten, 1978). Boyle (1974) found no typical photoreceptor cells in the aesthetes of *Lepidochitona cinerea* L., but he described "microvillous areas" and areas with "lamellate bodies". These very likely correspond to the rhabdomere and the agranular ER of the photoreceptor cells. This cell type is the only one in the aesthete that shows ultrastructural differences between light- and dark-adapted animals (Fischer, 1978a). Additionally, experiments with partially masked *C. olivaceus* clearly show that the shell valves contain photoreceptive elements (Fischer, unpub. data). As a common feature, photoreceptor cells seem to be a primary part in chiton aesthetes.

At first sight, it is astonishing that the shell valves contain so many, and simple, photoreceptive elements. In some species, aesthetes in certain shell areas have been transformed into eyes of various complexity (Boyle, 1969; Fischer, 1978a; Haas and Kriesten, 1978). Most species, however, have only the "normal" aesthete type. The situation could be comparable with other invertebrates, like the earthworm which avoid light during the day and feed at dawn and when it is dark. The earthworm also has many primitive light receptors dispersed in the skin. As behavioural studies show (Fischer, unpub. data), the photoreceptor cells in the aesthetes have a similar function. Most chiton species avoid bright sunlight and hide below stones or in the mud during the day. Chitons with masked shells do not exhibit such a behaviour (except species that also have photoreceptor cells in their girdle papillae, e.g. *Acanthochitona fascicularis*). Chitons that live in deeper water obviously have lost their photoreceptor cells. Baxter *et al.* (1987) found no photoreceptor cells in the aesthetes of *Tonicella marmorea* Fabricius.

The function of the micraesthetes is still completely obscure. Their high density in the shell valves suggests that they play an important role in the biology of the Polyplacophora. Among all species studied, only some of the lateral aesthetes in *Acanthochitona fascicularis* lack micraesthetes (Fischer, 1979). Baxter *et al.* (1987) showed that in *Tonicella marmorea*, the micraesthetes contain numerous lamellate granules. They suggest that micraesthetes and the megalaesthete produce periostracum material. This hypothesis has already been put forward by Nowikoff (1907). In all the species I studied, no secretory granules in the micraesthetes could be found. In addition, the subsidiary cap does not allow a penetration of material from the inside of the aesthete to the outside. In electrical recordings from the area underneath the subsidiary cap in *Chiton olivaceus*, no indication of a secretory process could be found under many different experimental conditions (Fischer, unpub. data). In other species, the subsidiary cap looks similar to that of *Lepidopleurus cajetanus* (Fischer and Renner, 1978; Haas and Kriesten, 1978) or are much thinner but without inner pores (Boyle, 1974). Both types can be present in different shell areas in certain species (Fischer, 1979). Baxter *et al.* (1987) showed that in *T. marmorea*, microvilli of the micraesthete cell protrude into the subsidiary cap. However, the distal surface of the cap also seems to be continuous in this species. In all species studied so far, the continuous part of the subsidiary cap is about 0.4 μm, irrespective to whether inner pores are present. Certainly there is a great need to study the aesthetes of species that differ in their ecology from the species studied so far, in order to gain a better understanding of the function of the micraesthetes.

ACKNOWLEDGMENTS

I am most grateful to Prof. G. A. Manley for correcting my English. I thank Birgit Seibel for technical assistance and Renate Kammerer for reading the manuscript. The present paper arose from a talk presented at the Symposium on the Biology of the Polyplacophora at the 1987 meeting of the American Malacological Union. I thank the AMU for financial support to attend that meeting.

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FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1986

ASSETS			
Current Assets			
AMU Operating Acct. # 3400934	$35,632.16		
Fortune Fed./C.D. # 0203206756	3,525.00		
Fortune Fed./C.D. # 0203206757	2,288.22		
Fortune Fed./C.D. # 0203127749	5,410.79		
AMU Endowment Fund # 3600459	759.65		
First Independence/C.D. # 80338	11,437.74		
San Antonio Acct. # 60005702	2,758.44		
Total Current Assets		$61,812.00	
Other Assets			
Total Other Assets		.00	
Total Assets			$61,812.00
LIABILITIES AND EQUITY			
Current Liabilities			
Total Current Liabilities		.00	
Equity			
Retained Earnings	$68,910.72		
Net Income (Loss)	7,098.72		
Total Equity		$61,812.00	
Total Liabilities and Equity			$61,812.00

	Current-Period Amount	Current-Period Ratio	Year-to-Date Amount	Year-to-Date Ratio
RECEIPTS:				
Memberships:				
Regular	$1,627.00	20.31	$ 8,446.86	18.88
Life	600.00	7.49	900.00	2.01
Sustaining	.00	.00	180.00	.40
Student (Regular)	63.00	.79	596.00	1.33
Corresponding	87.50	1.09	708.50	1.58
Clubs	110.00	1.37	508.50	1.14
Institutions	574.00	7.16	2,152.00	4.81
Total Memberships Receipts	$3,061.50	38.21	$13,491.86	30.15
Sales:				
AMU Bulletin/Back Issues	114.00	1.42	385.00	.86
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Bulletin Account	3,563.30	44.47	6,497.30	14.52
Total Sales Receipts	$3,922.30	48.95	$ 9,193.40	20.55
Other Receipts:				
Best Student Paper Donations	.00	.00	275.00	.61
Endowment Fund Donations	95.00	1.19	2,891.80	6.46
Endowment Fund Int. Withdrawn	.00	.00	1,192.72	2.67
Interest on All Accounts	845.24	10.55	3,908.69	8.73
Miscellaneous Donations	25.00	.31	325.35	.73
AMU Registration/Meeting	.00	.00	13,270.16	29.66
Publish Student Papers	10.00	.12	25.00	.06
Reprints	53.00	.66	174.00	.39
Total	$1,028.24	12.83	$22,062.72	49.31
Total Cash Receipts	$8,012.04	99.99	$44,747.98	100.01

	Current-Period Amount	Current-Period Ratio	Year-to-Date Amount	Year-to-Date Ratio
DISBURSEMENTS:				
AMU Bulletin/Postage, Printing	$ .00	.00	$16,963.23	37.91
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Filing Fee (California)	.00	.00	12.50	.03
Symposium Endowment Fund Dep.	.00	.00	2,900.00	6.48
Student Awards	.00	.00	500.00	1.12
Insurance	.00	.00	231.00	.52
Bank Charges	.00	.00	36.10	.08
Miscellaneous/Petty Cash	107.79	1.35	1,277.58	2.86
AMU Meeting	1,000.00	12.48	11,811.83	26.40
Bulletin Expenses	.00	.00	11,610.11	25.95
Membership Committee	.00	.00	160.00	.36
Total Disbursements	$1,176.52	14.69	$51,846.70	115.90
Net Income (Loss)	$6,835.52	85.30	$ 7,098.72	15.89

Respectfully submitted,
Anne Joffe, Treasurer 1986

AMERICAN MALACOLOGICAL UNION
Cancellaria gladiator
stephens 87
CHARLESTON, SOUTH CAROLINA 1988

54th ANNUAL MEETING
THE AMERICAN MALACOLOGICAL UNION
CHARLESTON, SOUTH CAROLINA
RADISSON FRANCIS MARION HOTEL
JUNE 19 - 26, 1988

The 54th annual meeting of the American Malacological Union will be held June 19 - 26, 1988, in Charleston, South Carolina. Charleston is a historical city, many parts of which have been beautifully restored as has the Radisson Francis Marion Hotel which is located downtown within walking distance of many restaurants, shops and other attractions. Charleston is easily accessible both by air and by interstate highway.

Three symposia are planned:

APPLICATIONS OF NUCLEIC ACID TECHNIQUES TO MOLLUSCAN SYSTEMATICS
(Organized by Dr. M. G. Harasewych, Dept. of Invertebrate Zoology,
Smithsonian Institution)

SYSTEMATICS AND EVOLUTION OF NON-MARINE MOLLUSKS
(Organized by Dr. Robert Hershler, Dept. of Invertebrate Zoology,
Smithsonian Institution)

HISTORY OF MALACOLOGY
(Organized by Dr. W. Backhuys, Leiden, The Netherlands)

In addition to the symposia, contributed papers and poster presentations, scheduled events will include a tour of historic Charleston, guided field trips to terrestrial and marine molluscan communities, an auction to benefit the symposium fund, and a banquet.

For further information please contact:
Richard E. Petit
President, AMU
P. O. Box 30
North Myrtle Beach, South Carolina 29582, USA

Western Society of Malacologists

ANNOUNCEMENT AND INVITATION TO PARTICIPATE

Symposium on Biogeography and Evolution of the Molluscan Fauna of the Galapagos Islands

21st Annual Meeting of the Western Society of Malacologists
Sonoma State University, Rohnert Park, California
17-21 July 1988

The Western Society of Malacologists maintains a long-standing tradition of emphasis on eastern Pacific molluscan faunas and in keeping with this tradition a symposium will be held on Monday, July 18, 1988 in Darwin Hall on the campus of Sonoma State University on the biogeography and evolution of the molluscan fauna of the Galapagos Islands. The purpose of this symposium is to bring together, some 150 years after Charles Darwin visited the Galapagos, researchers with interests in the taxonomic composition, biogeographic affinities, and evolutionary history of the living and fossil molluscan fauna of the Galapagos.

The following is a preliminary list of symposium participants; additional contributors are being solicited:

J. Wyatt Durham - University of California, Berkeley
William K. Emerson - American Museum of Natural History, New York
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Michel Montoya - San Jose, Costa Rica
Carole S. Hickman - University of California, Berkeley
Matthew J. James - Sonoma State University
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Contributions are welcome from neontologists and paleontologists with an interest in any aspect of taxonomic composition, biogeographic affinities, evolutionary relationships, stratigraphic distribution, geologic context, oceanographic setting or paleoecological relationships.

For further information, please contact:

Dr. Matthew J. James
WSM - Galapagos Symposium
Department of Geology
Sonoma State University
Rohnert Park, California 94928, U. S. A.
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CONTRIBUTOR INFORMATION

The *American Malacological Bulletin* serves as an outlet for reporting notable contributions in malacological research. Manuscripts concerning any aspect of original, unpublished research and detailed reviews dealing with molluscs will be considered for publication.

Each original manuscript and accompanying illustrations should be submitted with two additional copies for review purposes. Text must be typed on one side of 8½ x 11 inch bond paper, double-spaced, and all pages numbered consecutively with numbers appearing in the upper right hand corner of each page. Leave ample margins on all sides.

Form of the manuscript should follow that outlined in the *Council of Biology Editors Style Manual* (fifth edition, 1983). This can be purchased from the CBE, 9650 Rockville Pike, Bethesda, Maryland 20814, U.S.A.

Text, when appropriate, should be arranged in sections as follows:

1. Cover page with title, author(s) and address(es), and suggested running title of no more than 50 characters and spaces
2. Abstract (less than 5 percent of manuscript length)
3. Text of manuscript starting with a brief introduction followed by methodology, results, and discussion. Separate sections of text with centered subtitles in capital letters.
4. Acknowledgments
5. Literature cited
6. Figure captions

References should be cited within text as follows: Vail (1977) or (Vail, 1977). Dual authorship should be cited as follows: Yonge and Thompson (1976) or (Yonge and Thompson, 1976). Multiple authors of a single article should be cited as follows: Beattie *et al.* (1980) or (Beattie *et al.*, 1980).

All binomens should include the author attributed to that taxon the first time the name appears in the manuscript [e.g. *Crassostrea virginica* (Gmelin)]. This includes non-molluscan taxa. The full generic name along with specific epithet should be written out the first time that taxon is referred to in each paragraph. The generic name can be abbreviated in the remainder of the paragraph as follows: *C. virginica.*

In the literature cited section of the manuscript references must also be typed double spaced. All authors must be fully identified, listed alphabetically and journal titles must be unabbreviated. Citations should appear as follows:

Vail, V. A. 1977. Comparative reproductive anatomy of 3 viviparid gastropods. *Malacologia* 16(2):519-540.

Yonge, C. M. and T. E. Thompson. 1976. *Living Marine Molluscs.* William Collins Sons & Co., Ltd., London. 288 pp.

Beattie, J. H., K. K. Chew, and W. K. Hershberger. 1980. Differential survival of selected strains of Pacific oysters (*Crassostrea gigas*) during summer mortality. *Proceedings of the National Shellfisheries Association* 70(2):184-189.

Seed, R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms*, D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

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AMERICAN MALACOLOGICAL BULLETIN

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Cover. The intracapsular development of the muricid *Thais haemastoma canaliculata* is discussed in an article by Roller and Stickle in this volume, pages 189-197.

THE AMERICAN MALACOLOGICAL BULLETIN is the official journal publication of the American Malacological Union.

AMER. MALAC. BULL. 6(2)
October 1988

A COMPARATIVE STUDY OF LATE PREHISTORIC AND MODERN MOLLUSCAN FAUNAS OF THE LITTLE PIGEON RIVER SYSTEM, TENNESSEE

PAUL W. PARMALEE
FRANK H. McCLUNG MUSEUM
UNIVERSITY OF TENNESSEE
KNOXVILLE, TENNESSEE 37996, U. S. A.

ABSTRACT

Shells of freshwater gastropods and naiads recovered during the period June - December 1985 at the McMahan site, an aboriginal Mississippian (Dallas component: AD 1300-1600) mound and village complex situated adjacent to the West Prong Little Pigeon River, Sevierville, Sevier County, Tennessee comprised the largest prehistoric molluscan species assemblage from a small river in East Tennessee yet known. Six species of aquatic gastropods (7,411 shells) and 3,855 valves of freshwater mussels (Bivalvia: Unionidae), representing 45 species, were identified. Three of the six species of gastropods and 31 of the 45 species of mussels no longer occur in the Little Pigeon River system. For a 24 month period, June 1985 - May 1987, extant mussel populations in the West Prong Little Pigeon River adjacent to the McMahan site were monitored and shells collected, primarily from muskrat feeding stations. Only 11 species occur as viable populations; urbanization with its accompanying pollution probably represents the major cause in decimating the rich molluscan assemblage present during the late prehistoric period.

The McMahan site (40SV1), a multi-component, late prehistoric aboriginal village and mound complex situated adjacent to the West Prong Little Pigeon River, now within the city limits of Sevierville, Sevier County, Tennessee has aroused the interest of both amateur and professional archaeologists for over a century. The mound, Late Mississippian (Dallas component: AD 1300-1600) in origin, was reported to have been 125 yards (112 m) from the river and was 16 feet (4.8 m) in height and 240 feet (72 m) in circumference at the time Edward Palmer "opened" it in September, 1881 (Holmes, 1884). Palmer, then employed by the Bureau of Ethnology, recovered numerous lithic artifacts, ceramic vessels, engraved marine shell gorgets and three species of marine gastropods (listed as "*Marginella*?, *Oliva*?, *Busycon perversum*") that had been fashioned into beads and other objects. These were found as burial accouterments. Also listed in the 1884 report were three species of freshwater gastropods and four species of naiads.

Approximately 50 years passed before the mound was again excavated, this time by George Barnes, a relic collector from Tennessee who, like Palmer, removed numerous burials and quantities of lithic, ceramic and shell artifacts encountered in association with them. Except for surface collecting, little attention was given to the surrounding village areas until June - August 1978 when highway (TN Rt. 441 N Bypass) salvage excavations were carried out by Dr. Brian Butler for the Tennessee State Division of Archaeology. A series of test pits in the area to be affected by highway construction, ca. 1,500 m south of the mound, revealed former occupation of the site by Middle Woodland (Connestee: AD 300-600), Mississippian (Dallas: AD 1300-1600), and Cherokee (ca. AD 1650-1800) peoples. Bone from the various excavation units was generally well preserved, but shell was not. For this reason, and particularly because the majority of faunal material recovered came from pits and various other features that contained a mixture of Connestee, Dallas and/or Cherokee cultural materials, shell identifications and counts from these excavations were not incorporated in this study. It should be noted, however, no species were recovered in Butler's excavations that were not represented in the mound and adjacent village areas occupied by Dallas inhabitants.

METHODS

Owner of the property that included the mound and remaining former village areas of the McMahan site, Mr. James A. Temple of Sevierville arranged for the removal and sale of the site (but preserving most of the mound) for topsoil

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in the early 1980s. By the end of 1983, the soil on the north side of the mound had been removed and stockpiled. It was not possible to undertake salvage operations at that time, so only a small sample of bone and shell was recovered periodically from the stockpiles as they were removed over a period of months. In order to determine the perimeter of the mound along its south-facing edge so as not to destroy that portion of it during soil removal, Mr. Richard R. Polhemus, Research Associate, Frank H. McClung Museum, University of Tennessee, at the owner's request excavated a north - south trench (0.5 m wide, 21 m long, and 1.2 - 2.0 m deep from about mid-point to the south edge) to determine stages of construction and location of its outermost edge. Preservation of bone and shell from the mound fill was generally good to excellent; since the mound was built by Late Mississippian (Dallas) peoples and was part of the adjoining village complex from which the majority of faunal materials were recovered, shell from the trenching excavation was combined with the village material for this analysis.

Removal of the remaining village area south of the mound began in May 1985 and was completed by December of that year. Funds could not be made available for an organized archaeological salvage operation, so the only alternative, if any data were to be obtained from the wealth of both cultural and faunal materials present, was to recover as much as possible in the allotted time by the author's personal effort. I visited the site on 34 days during the period of soil removal, averaging ca. five hours each visit. On six occasions volunteers provided assistance with the excavation of material which was accomplished for the most part by shovelling and trowel sorting. The area was surface collected on each visit and the growing stockpiles of topsoil were also searched for cultural and faunal remains. Days in which soil removal was in progress, each newly exposed feature resulting from cuts (profiles) made by the heavy equipment was carefully examined for its content. Shell recovered from two five-foot test squares excavated at the south edge of the mound in October 1985 by Richard Polhemus was incorporated with those from the village excavations, surface collections, and mound. All recovered cultural and faunal specimens were washed and cleaned with a soft brush; after drying each collection lot was labelled and eventually a large series of the identifiable shells was also given the site designation number and date recovered. All specimens have been incorporated into the Frank H. McClung Museum collections, The University of Tennessee, Knoxville.

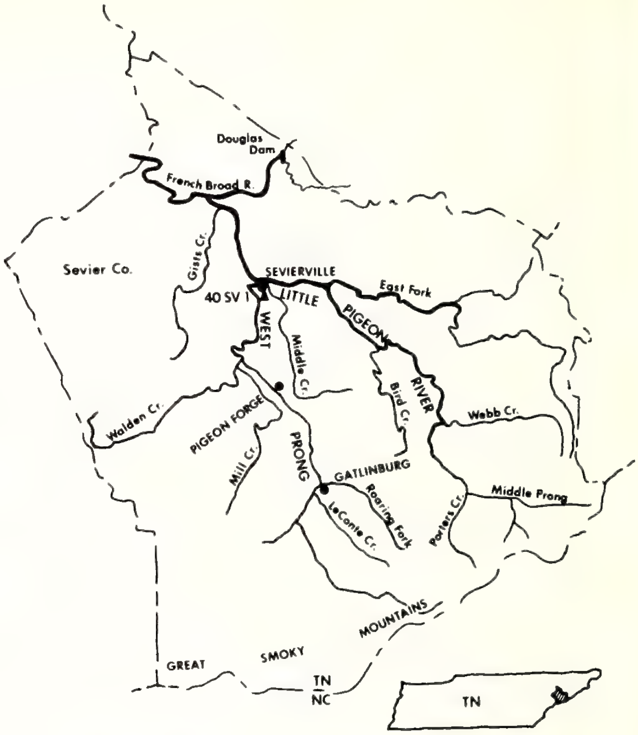

Fig. 1. Map showing the Little Pigeon River system and location of the McMahan site.

Recognizing the species diversity present in the archaeological molluscan samples from the McMahan site, a study of gastropod and freshwater mussel populations presently inhabiting the Little Pigeon River system was undertaken to determine possible changes in extant assemblages compared with those that existed in late prehistoric times. The Little Pigeon River is fed by two major tributaries, the East Fork, a small second order stream, and the West Prong Little Pigeon River, a fifth order stream only slightly less in size than the Little Pigeon itself (Fig. 1). Although the East Fork and the Little Pigeon were collected periodically, survey and collecting emphasis was placed on a ca. 0.7 km stretch of the West Prong Little Pigeon River that flowed above, adjacent to and below the McMahan site. Collecting trips were made in this section of the river at least twice each month for a 24-month period beginning in June 1985 and ending in May 1987. A total of 54 collecting and survey trips were made in this section of river during this period. Muskrats (*Ondatra zibethica* Linnaeus, 1766) inhabit the banks of the river and are the major predator of bivalves; utilization of this food resource is greatest during the winter months, ca. November through March. Shells obtained from muskrat feeding stations and those scattered along the river bottom, also probably discarded after the animal had been eaten by muskrats, formed the basis on which an evaluation of species occurrence and population density was made. Notations were made of live individuals and their number when encountered, but with the exception of less than a dozen specimens no living naiads were collected. Voucher specimens of most species represented have been placed in the Department of Malacology, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania and the Museum of Zoology, The Ohio State University, Columbus, Ohio; most of the remaining specimens obtained during this study are housed in the Malacology Collection, Frank H. McClung Museum.

RESULTS

SPECIES ACCOUNTS: GASTROPODA

Shells of six species of aquatic gastropods were recovered at the McMahan site (Table 1); 93% of the 7,411

Table 1. Freshwater gastropod shells identified from the Dallas component, McMahan site (40SV1), Sevierville, Sevier County, TN.

Species	No. of Shells	% of Shells
Campeloma cf. *decisum* (Say, 1816)	38	.51
Io fluvialis (Say, 1825)	374	5.05
Leptoxis praerosa (Say, 1821)	3,860	52.08
Lithasia (Angitrema) verrucosa (Rafinesque, 1820)	10	.13
Pleurocera canaliculatum (Say, 1821)	94	1.27
P. parvum (Lea, 1862)	3,035	40.95
Totals	7,411	99.99

specimens identified were those of *Pleurocera parvum* (Lea, 1862) and *Leptoxis praerosa* (Say, 1821), shells of the latter species representing over half of all the aquatic gastropods from the site. Most specimens of *Leptoxis* compared well with *L. praerosa*, many reaching a very large size characteristic of big river forms. Shell length (tip of the apex to the tip of the anterior aperture canal) of 20 of the largest specimens recovered had a mean of 18.4 mm. Although numerous small specimens of *Leptoxis* appeared intermediate between *L. praerosa* and the small river species *L. subglobosa* (Say, 1825) in shell characteristics, they could simply reflect juvenile stages of the former.

Specimens of the Spiny River Snail *Io fluvialis* (Say, 1825), comprised 5.0% of the aquatic snails. The taxonomy of this unique species, once widespread in the upper Tennessee River system, has been of special interest to malacologists for nearly 100 years. Adams (1915) provided the most definitive work on this gastropod up to that time; he recorded 14 species, characterized in part on shell size and obesity but especially on variation in spinosity. Generally, the small river species (forms) lacked spines while those populations established in big river shoals exhibited maximum development of spine size. Three distinct forms of *I. fluvialis* occurred at the McMahan site, and Parmalee and Bogan (1987) have discussed their taxonomy and ecological implications. Thirty-two percent lacked spines (small river form), 47% possessed low spines only on the last shoulder whorl ("intermediate" form) and 21% had well developed spines (big river form). It can be concluded that the West Prong Little Pigeon River possessed a varied substrate, shallow riffles and deep shoals within a 1.6-3.2 km stretch of the site that allowed the establishment of varied forms of *Io*.

Combined, shells of the three remaining species of gastropods represented at the McMahan site comprised <2% of the total. Although somewhat variable in habitat preference, *Pleurocera canaliculatum* (Say, 1821) and *Campeloma* cf. *decisum* (Say, 1816) can be found most often partially buried in mud or under matts of vegetation or debris near the shore. Although *Lithasia (Angitrema) verrucosa* (Rafinesque, 1820) can also occur in similar habitats, it apparently prefers rocks and submerged logs in stretches of river with pronounced current. Possibly they were less visible to the Indians while gathering mollusks than other species that inhabit more exposed river substratum. However, probable pristine river conditions at that time did not include a mud or silt substratum favorable to these species and therefore they were relatively uncommon to rare. Judging from the size range and numbers of gastropod shells recovered, occupants of the McMahan site gathered whatever was available.

SPECIES ACCOUNTS: PELECYPODA

The number of naiad species represented in the molluscan assemblage from the McMahan site relative to the quantity of valves recovered and period of accumulation is unequaled among other archaeologically derived samples from Tennessee. A total of 3,855 valves, representing a minimum of 45 species (Table 2), was identified to the generic and/or species level. Forty-three species of freshwater mussels were identified from the Clinch River Breeder Reactor Plant site, Roane County (Parmalee and Bogan, 1986), but this involved a sample of ca. 23,900 valves and a time span of accumulation of at least 1,500 years. Parmalee *et al.* (1982) recorded 45 species of naiads from 15 aboriginal sites in the Chickamauga Reservoir (Tennessee River), based on the identification of nearly 27,900 valves, but again this involved approximately a 1,500 year time period. Nearly 3,800 valves, representing 38 species of naiads, were recorded by Bogan (1980) from Dallas and Cherokee occupational zones at the Toqua site, Little Tennessee River, Monroe County. The diverse naiad assemblage reflected in the McMahan site molluscan sample is indicative of the rich late prehistoric populations that inhabited this small river and provides some evidence of the varied aquatic habitats that apparently once existed in the West Prong Little Pigeon River.

Amblema plicata (Say, 1817): Parmalee and Bogan (1986) noted that the Three-ridge Mussel possibly could not have been as numerous in prehistoric times as it is at present, judging by the relatively small numbers (2.19% of ca. 23,900 valves) recovered at the Clinch River Breeder Reactor Plant site. It accounted for <1% of 27,875 valves identified from 15 sites in the Chickamauga Reservoir (Parmalee *et al.*, 1982). Although valves of both juveniles and adults were noted in the naiad sample from the McMahan site, their number accounted for <1% of the total.

Fusconaia Simpson, 1900: Valves of both forms of *F. barnesiana* (Lea, 1838), the Tennessee Pigtoe *F. barnesiana tumescens* (Lea, 1845), a heavy, swollen shell, and *F. barnesiana bigbyensis* (Lea, 1841), a thinner, more compressed form occurred in the McMahan site samples. Ortmann (1918) noted that "...we have the phenomenon that flat and compressed forms are found in the headwaters, swollen forms in the larger rivers, with the intergrades between them in rivers of medium size." Ortmann (1918) reported both forms from the Little Pigeon River; combined, shells of both forms and "intergrades" totalled 347, representing 9.0% of the sample.

Nearly 11% of all identified valves were those of the Long Solid *Fusconaia subrotunda* (Lea, 1831), and the number of shells (409) of this species in the McMahan site sample ranked second in the total assemblage. At least two distinct forms were present, one of which Ortmann (1918)

Table 2. Freshwater mussels identified from the Dallas component, McMahan site (40SV1), Sevierville, Sevier County, TN. [I = Interior Basin (Mississippi); C = Cumberlandian; U = Unknown].

Species	No. of Valves	%	Region of Origin
Amblema plicata (Say, 1817)	22	.57	I
Fusconaia barnesiana (Lea, 1838)	347	9.00	C
F. subrotunda (Lea, 1831)	409	10.60	U
Quadrula cylindrica (Say, 1817)	6	.15	U
Q. pustulosa (Lea, 1831)	5	.12	I
Q. sparsa (Lea, 1841)	50	1.29	C
Cyclonaias tuberculata (Rafinesque, 1820)	74	1.91	I
Elliptio crassidens (Lamarck, 1819)	23	.59	I
E. dilatata (Rafinesque, 1820)	70	1.81	U
Hemistena lata (Rafinesque, 1820)	1	.02	C
Lexington dolabelloides (Lea, 1840)	96	2.49	C
Plethobasus cooperianus (Lea, 1834)	11	.28	I
P. cyphyus (Rafinesque, 1820)	46	1.19	I?
Pleurobema cordatum (Rafinesque, 1820)	33	.85	I
P. oviforme (Conrad, 1834)	24	.62	C
P. plenum (Lea, 1840)	21	.54	I
P. cf. *rubrum* (Rafinesque, 1820)	1	.02	I
Alasmidonta marginata (Say, 1819)	1	.02	I
A. viridis (Rafinesque, 1820)	31	.80	I
Anodonta, A. cf. *grandis* (Say, 1829)	1	.02	I
Lasmigona costata (Rafinesque, 1820)	8	.20	U
L. holstonia (Lea, 1831)	5	.12	C
Actinonais ligamentina (Lamarck, 1819)	148	3.83	I
Toxolasma lividus (Rafinesque, 1831)	131	3.39	C
Epioblasma arcaeformis (Lea, 1831)	26	.67	C
E. brevidens (Lea, 1834)	1	.02	C
E. capsaeformis (Lea, 1834)	42	1.08	C
E. cf. *florentina* (Lea, 1857)	1	.02	C
E. haysiana (Lea, 1833)	23	.59	C
E. stewardsoni (Lea, 1852)	2	.05	C
E. torulosa (Rafinesque, 1820)	11	.28	C
Lampsilis fasciola (Rafinesque, 1820)	385	9.98	I
L. ovata (Say, 1817)	79	2.04	I
Lemiox rimosus (Rafinesque, 1831)	8	.20	C
Ligumia recta (Lamarck, 1819)	2	.05	U
Medionidus conradicus (Lea, 1834)	172	4.46	C
Obovaria subrotunda (Rafinesque, 1820)	9	.23	I
Potamilus alatus (Say, 1817)	9	.23	I
Villosa iris (Lea, 1830)	167	4.33	C
V. trabilis (Conrad, 1834)	183	4.74	C
V. vanuxemensis (Lea, 1838)	302	7.83	C
V. spp.	200	5.18	—
Cyprogenia stegaria (Rafinesque, 1820)	5	.12	U
Dromus dromas (Lea, 1834)	32	.83	C
Ptychobranchus fasciolaris (Rafinesque, 1820)	124	3.21	U
P. subtentum (Say, 1825)	508	13.17	C
Totals	3,855	99.74	

recorded as *F. pilaris* (Lea, 1840) and viewed it as "...the upper Tennessee representative of *F. subrotunda* Lea of the Ohio drainage, and it could be merely a dwarfed, globular form of the latter." Apparently this form, which dominated the McMahan site *F. subrotunda* "complex," was typical of the large river such as the Tennessee and the lower Little Tennessee and French Broad. A few valves of the compressed headwaters form of this species were recovered. The Long Solid appears to have been a major component of the West Prong Little Pigeon River prehistoric naiad fauna and the predominance of the thick globular form suggests stretches of large river habitat.

Quadrula Rafinesque, 1820: Three species belonging to this genus were represented in the McMahan site naiad assemblage; however, only six valves of the Rabbit's Foot *Quadrula cylindrica* (Say, 1817) and five valves of the Pimpleback *Q. pustulosa* (Lea, 1831) were recovered. At present both can be found locally common in small to large river habitats throughout the state, but it has been noted (Parmalee *et al.*, 1982; Parmalee and Bogan, 1986) that these were uncommon shells in the Tennessee River system in aboriginal times. Fifty valves of the Appalachian Monkey Face *Q. sparsa* (Lea, 1841), a species generally associated with small tributary streams of the upper Tennessee River drainage, occurred in the archaeological sample. It is a rare species and remaining populations appear limited to the unimpounded stretches of the Powell and Clinch rivers in upper East Tennessee and southwestern Virginia. Parmalee and Bogan (1986) reported 113 valves of *Q. sparsa* from Middle Woodland and Mississippian components at the Clinch River Breeder Reactor Plant site, Roane County, Tennessee and a single valve of this species was recovered at the Starnes site, a historic Cherokee farmstead along the lower Tellico River, Monroe County, Tennessee (Parmalee and Klippel, 1984).

Cyclonaias tuberculata (Rafinesque, 1820): The Purple Warty-back is a widely distributed and locally common mussel in Tennessee in both small and large rivers. As evidenced by the quantity of valves recovered from aboriginal sites, it was an abundant shell also in prehistoric times. For example, Morrison (1942), in his analysis of shells from the Pickwick Basin mounds (Tennessee River, northern Alabama), commented that it "...was extremely abundant in all the mounds. It constituted one of the major fractions of the mussel fauna that was used for food in building up the shell deposits." Although there appears to have been a viable population present prehistorically in the West Prong Little Pigeon River, the number of valves recovered at the McMahan site (74, <2% of the total) suggests it was not abundant.

Elliptio Rafinesque, 1820: Shells of the Elephant's Ear *Elliptio crassidens* (Lamarck, 1819) and the Spike *E. dilatata* (Rafinesque, 1820) have been recovered in considerable numbers at aboriginal sites located along large rivers such as the Tennessee (see Parmalee *et al.*, 1982). *E. crassidens* is typically a large river species where it can become abundant locally, but occasionally a few individuals will become established in small- to medium-sized streams such as the West Prong Little Pigeon River. The Spike, on the other hand, is often the most abundant species present in small rivers. Although there were three times the number of shells of *E. dilatata* than *E. crassidens* in the McMahan site sample, suggesting a predominance of small river habitat, combined they accounted for <3% of the total.

Hemistena lata (Rafinesque, 1820): The Cracking Pearly Mussel was reported to have occurred in the Ohio, Cumberland and Tennessee River systems. Ortmann (1918) commented that "It is undoubtedly a rare shell;" in some rivers such as the upper Clinch, however, it is locally common (Ahlstedt, 1984). It appears to have been a rare species in the West Prong Little Pigeon River during the time the McMahan site was occupied as evidenced by the recovery of only one valve.

Lexingtonia dolabelloides (Lea, 1840): The former ecological environs of the Slab-side Mussel included shoal areas of the Tennessee River downstream at least as far as Pickwick Landing Basin in northern Alabama and its larger tributaries in upper East Tennessee. Impoundment has eliminated its habitat in the Tennessee River, and *L. dolabelloides* is now limited to and is generally uncommon in rivers such as the Duck, Clinch and Powell. Ortmann (1918) observed that "...here we have a case where a swollen form (*dolabelloides*) is found in the larger rivers, and a compressed one (*conradi*) in the smaller stream, with the intergrades existing between them." This condition was apparent in the McMahan site material, where valves of this species comprised ca. 2.5% of the total, but the thick-shelled, swollen form predominated.

Plethobasus Simpson, 1900: Combined, shells of *Plethobasus cooperianus* (Lea, 1834), the Orange-footed Pimple-back and *P. cyphyus* (Rafinesque, 1820), the Sheepsnose, totaled ca. 2.5% of the naiad sample. In Tennessee the former species was considered an inhabitant of the deep stretches of the Cumberland and Tennessee rivers and their large tributaries. With reference to *P. cooperianus*, Ortmann (1918) stated that "I also found it in French Broad River, at Boyd Creek, Sevier County, Tenn. Records from 'Holston River' probably refer to the Tennessee, at any rate, it must be a rare shell above Knoxville." Only 11 valves of it were identified while 46 specimens of *P. cyphyus*, a shell that can be found in small rivers as well as large, were recovered. Valves of the Sheepsnose from the McMahan site appeared intermediate between the typical large river form that is drawn out posteriorly with a distinct row of pronounced knobs, and the small river form with the radial row of knobs on the disk poorly developed and nearly obliterated in some specimens.

Pleurobema Rafinesque, 1820: A total of 79 valves (2.0% of the sample), representing four species in this genus, were recovered in the sample. Three of these, *P. cordatum* (Rafinesque, 1820), Ohio River Pigtoe; *P. plenum* (Lea, 1840), Rough Pigtoe; and *P. rubrum* (Rafinesque, 1820), Pyramid Pigtoe, are generally considered large river, deep water species that only rarely become established in small- to medium-size streams. Of the approximately 40,500 valves (ca. 50 species) identified from 15 aboriginal sites in the Chickamauga Reservoir (Tennessee River), those of these three species of *Pleurobema* accounted for nearly 13% of the total (Parmalee *et al.*, 1982). Although these and certain other big river species are represented in the McMahan sample, their limited numbers suggest the probability that stretches of deep water habitat in the West Prong Little Pigeon River were limited compared with greater riffle and shoal areas typical of small- to medium-size rivers.

The fourth species of *Pleurobema* recorded from the site, *P. oviforme* (Conrad, 1834), the Tennessee Clubshell, is restricted to the upper Cumberland and Tennessee River drainages and is one that typically inhabits the smaller streams and rivers. The taxonomic position of this species is not entirely clear: it is characteristic of small rivers of the upper Tennessee River drainage and probably represents *P. clava* (Lamarck, 1819) of the Ohio and lower Cumberland and Tennessee rivers. Ortmann (1918) lists *P. oviforme argenteum* (Lea, 1841) as "...the compressed form of *oviforme*, peculiar to the headwaters and other small streams. It also generally attains a larger size than the typical *oviforme*, and is more rhomboidal in outline. It is in Little Pigeon River, at Sevierville, Sevier Co., TN., but not very well developed here, the majority of the specimens belonging to *oviforme*." Ortmann implied by this that the medium-sized river form *P. oviforme* closely resembled the upper Ohio River form of *P. clava*, but he made note of the extreme shell variability, a condition apparent in the McMahan site specimens.

Alasmidonta Say, 1818: Shells of two species representative of this genus were recovered at the McMahan site. One, the Elk Toe *Alasmidonta marginata* (Say, 1819), is widespread throughout the small streams and medium-size rivers of East Tennessee. However, it appears to have been a rare shell prehistorically in the West Prong Little Pigeon River as only one right valve of a mature individual was recovered. The other species, the Slipper Shell *A. viridis* (Rafinesque, 1820), although not abundant (31 valves) suggests a former viable population at this point in the river. Ortmann (1918) states that it, *A. (Pressodonta) minor* Lea, 1845, is "A characteristic small creek species, locally abundant. It is found all over the region, but strictly avoids the medium-sized and larger rivers." He recorded it from the Little Pigeon River at Sevierville.

Anodonta, cf. *A. grandis* (Say, 1829): Although at present one of the most widely distributed and locally abundant shells throughout impounded stretches of Tennessee rivers, a slow current and mud/silt substratum most favorable to the Common Floater was probably limited prehistorically. Of interest is the statement by Ortmann (1918) that "No *Anodonta* has ever been reported from the upper Tennessee region"; however, he does make reference to two specimens (in the collection of Bryant Walker) collected in a small pond near the French Broad River eight miles above Knoxville. Bogan (1980) identified a single valve of *A. grandis*, found as a burial accouterment, from the Toqua site, Little Tennessee River, Monroe County. In his treatment of the mollusks from Pickwick Basin (Tennessee River), Morrison (1942) listed *A. grandis*, along with four other species in the subfamily Anodontinae, as "...present in small numbers only." No valves of *A. grandis* were identified from the thousands of naiads recovered from aboriginal sites along the Cumberland, Clinch and Tennessee rivers in Middle and East Tennessee (Parmalee *et al.*, 1980, 1982; Parmalee and Bogan, 1986). Only one incomplete right valve from the McMahan site suggests that *A. grandis* was prehistorically a rare shell in the West Prong Little Pigeon River.

Lasmigona Rafinesque, 1831: *Lasmigona costata* (Rafinesque, 1820), the Fluted Shell, occurs in both large rivers like the Cumberland and Tennessee and in small- to medium-sized rivers like the middle Duck and the upper Powell and Clinch. Ahlstedt (1984) noted that it "...is an extremely common species in the upper Clinch in Tennessee and Virginia." Judging by certain extant unmodified stretches of the West Prong Little Pigeon River (Fig. 2), assuming them to be not unlike prehistoric conditions, it would seem this river would have provided favorable habitat for *L. costata*. However, only eight valves were recovered at the McMahan site. *L. holstonia* (Lea, 1831), the Tennessee Heelsplitter, a species often found locally abundant in small and/or headwater streams, was also poorly represented at the site (5 valves, 3 individuals). All three were juveniles, the largest measuring 35.5 mm total length. Ortmann (1918) recorded it for the Little Pigeon River, Sevier County.

Actinonaias ligamentina (Lamarck, 1819): Prehistorically the Mucket was widely distributed and common throughout the major rivers in Tennessee such as the Clinch, Holston, Tennessee, French Broad, and Cumberland. At present, however, except for local populations in these rivers (primarily the Holston), populations of *A. ligmentina* are restricted mainly to the unimpounded upper stretches of the Clinch and Powell rivers in East Tennessee. In archaeological context, the percentage of shells of the Mucket varied from 7.5% of those recovered in 15 sites in the Chickamauga Reservoir (Tennessee River) (Parmalee *et al.*, 1982), and 13.5% at the Clinch River Breeder Reactor Plant site (Parmalee and Bogan, 1986), to nearly 16% in two sites along the middle Cumberland River (Parmalee *et al.*, 1980). The total of 148 valves, representing 3.8% of all identified shells recovered at the McMahan site, suggests a former viable population of this mussel in the West Prong Little Pigeon River. A right valve of a mature individual exhibited a high degree of polish on its external surface; this modification possibly resulted from its use as some form of shaping or smoothing tool in the manufacture of ceramic vessels.

Toxolasma lividus (Rafinesque, 1831): A total of 131 shells belonging to the genus *Toxolasma* were assigned to the species *T. lividus*, the Little Purple. With respect to the *Toxolasma* complex in this region, the comments of Ortmann (1918) are appropriate: "What Lea has described as *U. moestus* (from French Broad River, Tenn.) undoubtedly is this *[T. lividus]*: I have specimens from Little Pigeon River (tributary to French Broad), which are fully identical with *moestus*. *U. [Toxolasma] cylindrellus* Lea (Duck River, TN.) is in shape absolutely identical with *T. lividium*; however, it differs by paler color of epidermis and nacre." In light of these comments, it is possible that some of the specimens from the McMahan site are *T. cylindrellus* (Lea, 1868), assuming it is a good species. Many valves of *Toxolasma* from the site still exhibited a faded but uniform purple nacre. This small naiad appears to have been fairly common prehistorically in the West Prong Little Pigeon River.

Epioblasma Rafinesque, 1831: Seven species belonging to this genus were represented in the molluscan sample from the McMahan site, but combined the number of shells totaled only 106, 3.0% of all identified valves. Three of these species, *Epioblasma arcaeformis* (Lea, 1831), the Sugar Spoon; *E. haysiana* (Lea, 1833), the Acornshell; and *E. stewardsoni* (Lea, 1852), the Cumberland Leafshell, are now considered extinct (Stansbery, 1971). The Yellow Blossom *E. florentina* (Lea, 1857), represented at the McMahan site by a single right valve of a male and identified as probably *E. f.* form *florentina* based on the descriptions of Ortmann (1918) and Bogan and Parmalee (1983), is probably close to extinction. The large river, nodular form of the Tubercled Blossom

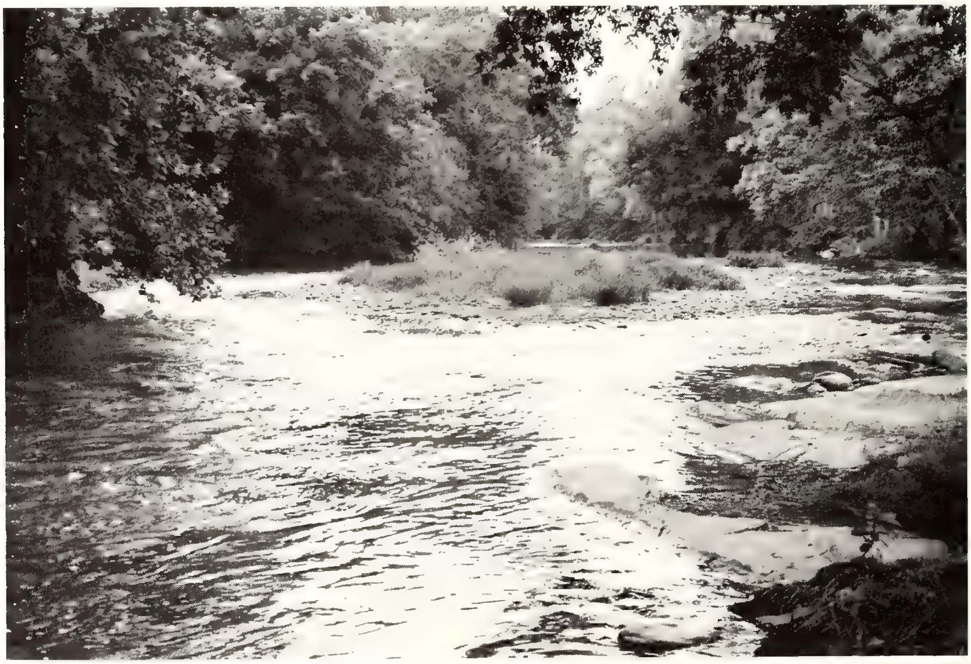

Fig. 2. View of West Prong Little Pigeon River, north edge of Pigeon Forge, TN. Unmodified stretch of river, but at present poor mussel habitat.

E. torulosa torulosa (Rafinesque, 1820), can also be considered extinct. Ortmann (1918) commented that *E. arcaeformis* was found in large and medium-sized rivers and that it was present in the French Broad River at Boyd Creek, Sevier County. *E. stewardsoni* also occurred in shoal areas of the larger rivers, but, unlike the once abundant *E. t. torulosa*, it was apparently "A rare species" (Ortmann, 1918).

Of the seven species of *Epioblasma* identified from the site, valves of *Epioblasma capsaeformis* (Lea, 1834), the Oyster Mussel, were the most numerous (42). This mussel is at present locally abundant in the upper unimpounded stretches of the Clinch and Powell rivers; it also can be found in limited numbers in other small- to medium-sized rivers in Middle and East Tennessee. Ortmann (1918) reported it from the Little Pigeon River. Surprisingly, only one valve of the Cumberlandian Combshell *E. brevidens* (Lea, 1831), was recovered at the McMahan site; it was widely distributed and locally common in medium-sized rivers such as the Big South Fork Cumberland, Clinch and Powell in the Cumberland and Tennessee River drainages of East Tennessee.

Lampsilis Rafinesque, 1820: A total of 385 valves of the Wavy-rayed Lampmussel *Lampsilis fasciola* (Rafinesque, 1820), representing ca. 10% of the naiad sample, was recovered at the McMahan site. Ortmann's (1918) comment that this species of *Lampsilis* is "practically everywhere in the larger rivers as well as in smaller streams, but apparently more abundant toward the headwaters" is appropriate relative to the West Prong Little Pigeon River. On the basis of the archaeological record, it was a very common shell at the time the McMahan site was occupied. However, extensive naiad samples from large rivers in East Tennessee indicate that *L. fasciola* was rare, at least in the stretches near the sites: Cumberland River, 2 sites, 7 specimens in a sample of 827 valves (.12%) (Parmalee *et al.*, 1980); Tennessee River, 15 sites, 3 specimens in a sample of 27,875 valves (.01%) (Parmalee *et al.*, 1982); Clinch River, 1 site, 21 specimens in a sample of 23,905 valves (.09%) (Parmalee and Bogan, 1986).

Seventy-nine valves of *Lampsilis ovata* (Say, 1817), the Pocketbook, about 2% of the sample, were found at the McMahan site. The "typical" shell of *L. ovata* is characterized by the distinct and sharp posterior ridge and, according to Ortmann (1918), it is restricted to the larger rivers. However, he points out (Ortmann, 1918) that "All along its range, and chiefly *above* Knoxville, it is accompanied by the var. *ventricosa*, and intergrades with it;" specimens examined from the Little Pigeon River, Sevierville were identified by Ortmann as *L. ovata ventricosa*. However, all valves from the McMahan site complete enough to ascertain the angle of the posterior ridge were *L. ovata* and not *L. o. ventricosa* (more rounded, lacking the sharp-angled posterior ridge). Although less abundant than *L. fasciola*, there appears to have been a viable population of *L. ovata* in the West Prong Little Pigeon River during aboriginal occupation of the McMahan site.

Lemiox rimosus (Rafinesque, 1831): A species of the upper Tennessee River drainage, the Birdwing Pearlymussel formerly inhabited shoals of the large rivers as well as small streams, but it is at present restricted to local populations in medium-sized rivers such as the Duck and upper Clinch and Powell. Parmalee and Bogan (1986) recorded 623 valves (2.6% of the total) of this small mussel in a sample of 23,905 shells from the Clinch River Breeder Reactor Plant site, but only 24 (.09% of a total of 27,875 valves) were recovered from 15 sites reported from the Chickamauga Reservoir (Tennessee River) by Parmalee *et al.* (1982). In his study of mollusks from the Pickwick Basin, Morrison (1942) reported *L. rimosus* "...throughout the mounds, but...nowhere in great abundance." Ortmann (1918) considered it a rare shell and, except for one local population in the Duck River (Maury County), Ahlstedt (1984) also noted that it could not be found in any great numbers. Prehistorically it must have been a rare species in the West Prong Little Pigeon River as only eight specimens were recovered in the McMahan site sample.

Ligumia recta (Lamarck, 1819): the Black Sandshell is widely distributed from Pennsylvania to Minnesota south to Oklahoma and Alabama (Burch, 1975); it inhabits primarily medium-sized to large rivers where it may become locally numerous. With the recovery of only two valves at the McMahan site, it must have been a rare shell in the West Prong Little Pigeon River during the time the site was occupied. The assumption can be made that in the case of the Black Sandshell, like other species represented by only one or a very few valves, individuals became established from time to time but, for whatever reason(s), the river proved unsuitable for the development of viable populations.

Medionidus conradicus (Lea, 1834): The Cumberland Moccasin is a species endemic to the Upper Cumberland and Tennessee River systems, and its distribution was characterized by Ortmann (1918) as "Very abundant in the headwaters and in small streams generally, but quite rare in the larger rivers." In a sample of 761 identified mussel shells from Cheek Bend Cave, a multicomponent (Archaic-Woodland: ca. 7,000-1,000 BP) rockshelter site along the Duck River, Maury County, valves of *M. conradicus* (100) comprised 13.1% of the sample (Parmalee and Klippel, 1986). A total of 172 shells of this species (4.5% of the sample) were recovered at the McMahan site.

A study of species composition and abundance of extant naiad taxa in the West Prong Little Pigeon River adjacent to the McMahan site covered a two year period from June 1985 through May 1987. Results of this investigation will be considered in more detail in this paper under PRESENT NAIAD POPULATIONS: LITTLE PIGEON RIVER SYSTEM, but in the case of aboriginal vs extant *Medionidus* specimens, a brief comment here is appropriate. Only 12 individuals of the Cumberland Moccasin were obtained (at muskrat feeding stations) during this two year period. The right valve of each was measured (mm): Range, 46.0 - 62.0; Mean, 55.23. During the initial identification process, it was noted that the entire series of *Medionidus* from the site was made up of small specimens. Length of the complete valves (N=29) was measured (mm): Range, 24.5 - 42.5; Mean, 32.08. It appears that individuals in the modern population of *M. conradicus* reach a considerably larger mean size (55.23 mm, modern, vs. 32.08 mm, archaeological) than did those from prehistoric context; the largest specimen from the McMahan site had not attained the size of the smallest individual recovered in

1985-87. It is reasonable to assume the Indian would have gathered the large individuals as well as the small had they been present, so for whatever reason(s) the prehistoric population of *M. conradicus* in the West Prong Little Pigeon River consisted of individuals that did not attain the size of those found in living populations.

Obovaria subrotunda (Rafinesque, 1820): Once widespread throughout the Ohio, Tennessee and Cumberland river systems, the range and population densities of the Round Hickory Nut are now greatly reduced. This species is adaptable to both large river and small stream habitats. Ortmann (1918) considered it rare in the upper Tennessee region, including the small stream form *O. subrotunda levigata* (Rafinesque, 1820), in tributaries of the Tennessee, Holston and French Broad rivers above Knoxville. It appears to have been a rare shell in the West Prong Little Pigeon River as only nine valves were recovered at the McMahan site.

Potamilus alatus (Say, 1817): The Pink Heelsplitter occurs throughout the Mississippi drainage from Pennsylvania south to Arkansas, Tennessee and Alabama (Burch, 1975). Often an abundant shell locally in large and medium-sized rivers, it occurs less commonly in small streams. Like the preceding species, *P. alatus* was an uncommon to rare mussel (nine individuals) prehistorically in the West Prong Little Pigeon River.

Villosa Frierson, 1927: A total of 852 valves, representing at least three species within this genus, amounted to 22.0% of all freshwater mussel shells identified from the McMahan site. All are typical of small- to medium-sized streams and locally they can occur in large numbers. For example, Ahlstedt (1981) noted that *Villosa perpurpurea* (Lea, 1861) [probably a purple-nacre form or variety of *V. trabilis* (Conrad, 1834)] was "common" in Copper Creek, VA. Parmalee and Klippel (1984) found *V. iris* (Lea, 1829), the Rainbow, and *V. vanuxemensis* (Lea, 1838), the Mountain Creekshell, to be the two most common mussels inhabiting the Tellico River, Monroe County, TN. Of the 1,125 specimens recorded from this river, these two species of *Villosa* comprised 68.4% of the sample.

Villosa trabilis, the Cumberland Bean, is a small- to medium-sized river species that is known from the upper Tennessee and Cumberland River drainages, although its distribution appears spotty. For example, it is one of the few species still surviving as a viable population in the Obed River, Cumberland County, TN on the Cumberland Plateau. Both the Rainbow and the Mountain Creekshell are common and widely distributed in the streams of East and, to a somewhat lesser extent, Middle Tennessee; the latter species is one of the few naiads that often becomes abundant in the headwaters. Judging by the number of identifiable valves (see Table 2) recovered, *V. vanuxemensis* was the most common species of *Villosa* in the West Prong Little Pigeon River during the period of site occupation. However, all three taxa had well established viable populations and their abundance in the archaeological record indicates former extensive stretches of fast current and riffles with a substrate composed of cobbles, gravel and coarse sand.

Cyprogenia stegaria (Rafinesque, 1820): The Fanshell was once found rather sparingly throughout the upper Tennessee and Cumberland rivers of Tennessee. It has been poorly represented in some aboriginal molluscan faunas including two recorded by Parmalee *et al.* (1980) from the Cumberland River and at 15 sites along the Tennessee (Chickamauga Reservoir, Parmalee *et al.*, 1982). However, Morrison (1942) reported that it was "...found in moderate abundance, in nearly all the samples studied [from the Pickwick Basin mounds. Tennessee River]." Ahlstedt (1984) found *C. irrorata* to be a relatively common shell in the upper Clinch River in Tennessee and Virginia. Ortmann (1918) noted that "...in the lower Clinch it is quite abundant"; at the Clinch River Breeder Reactor Plant site valves of the Fanshell totaled 2,463, 10.3% of the total naiad sample (Parmalee and Bogan, 1986). Although the West Prong Little Pigeon River would appear to have been suitable for the establishment of a viable population of this mussel, judging by the archaeological species assemblage recovered and local populations that presently exist in rivers such as the upper Clinch, the occurrence of only five valves of *C. irrorata* in the McMahan site molluscan sample attest to its former rarity there.

Dromus dromas (Lea, 1834): Prehistorically the Dromedary Pearlymussel was one of the most abundant shells inhabiting the Cumberland and Tennessee River systems. Approximately 9,800 valves, comprising 35.25% of the naiad sample from 15 sites in the Chickamauga Reservoir (Parmalee *et al.*, 1982), and 111 valves (13.42% of the sample) from two sites along the middle Cumberland River in Tennessee (Parmalee *et al.*, 1980) are two examples attesting to its former abundance. Moreover, Morrison (1942), with reference to the Pickwick Basin mounds, Tennessee River, northern Alabama commented that "...*dromas* must have been very abundant here previously. These specimens are of good size for the species, and made up a major part of the total mussel fauna gathered for food." Although not common at the McMahan site (32 identified valves, <1.0% of the sample), apparently a few individuals and possibly small populations became established from time to time. Except for six shells of juveniles, all specimens of *D. dromas* from the site were the typical big river form, swollen with a large knob or lump on each valve.

Ptychobranchus Simpson, 1900: Shells of two species belonging to this genus, *Ptychobranchus fasciolaris* (Rafinesque, 1820), the Kidneyshell, and *P. subtentum* (Say, 1825), the Fluted Kidneyshell, were recovered at the McMahan site and together totaled about 16% of the naiad sample. However, shells of the latter species made up slightly over 13%. Ortmann (1918) stated that the Kidneyshell was "widely and uniformly distributed over the upper Tennessee region, but nowhere in great numbers." After nearly 70 years this statement is still a fairly accurate evaluation of its status in Tennessee, although impoundment and increased pollution and silting problems have brought about some changes. Recovery of 124 shells of *P. fasciolaris*, both juveniles and adults, suggests a former viable population of this species in the West Prong Little Pigeon River.

The most numerous shell recovered in the McMahan site naiad sample was the Fluted Kidneyshell. A total of 508 valves were identified as *Ptychobranchus subtentum*; in addition, of the nearly 1,000 indeterminate fragmented valves, close to 200 of these could also have been referable to this species judging by incomplete tooth/hinge line and fluted posterior slope sections. *P. subtentum* is an inhabitant of small- to medium-sized streams of the upper Cumberland and Tennessee River systems, becoming most abundant toward the headwaters. It is, for example, a very common shell locally in the unimpounded stretches of the Powell and Clinch rivers in northeastern Tennessee and southwestern Virginia. At the time the McMahan site was occupied, the Fluted Kidneyshell was an abundant mussel in the naiad assemblage and, in addition to its value as a food resource, the Indian utilized (almost exclusively) shells of this species as some type of tool (Fig. 3). Approximately 175 valves exhibited modification to the posterior ventral margin; the shells appeared to have been used as some form of scraper, the ventral edge of each having been ground or worn down at an angle toward the posterior end. Riggs (1987) illustrates two valves of *Actinonaias ligamentina*, recovered at an early 19th century Cherokee farmstead (Bell Rattle Cabin site, Monroe County, TN), that were modified in a like fashion as those from the McMahan site. He attributed the modified edges to the shells use as a potter's tool; i.e. the valves were used to scrape and smooth clay vessels before they were fired. Harrington (1922) mentions that "...the cherokee formerly used mussel-shells and a marine shell, probably some species of *Cardium*, for this purpose" (pottery smoothing tool). Shells of *P. subtentum* from the McMahan site were obviously preferred for this function as only three

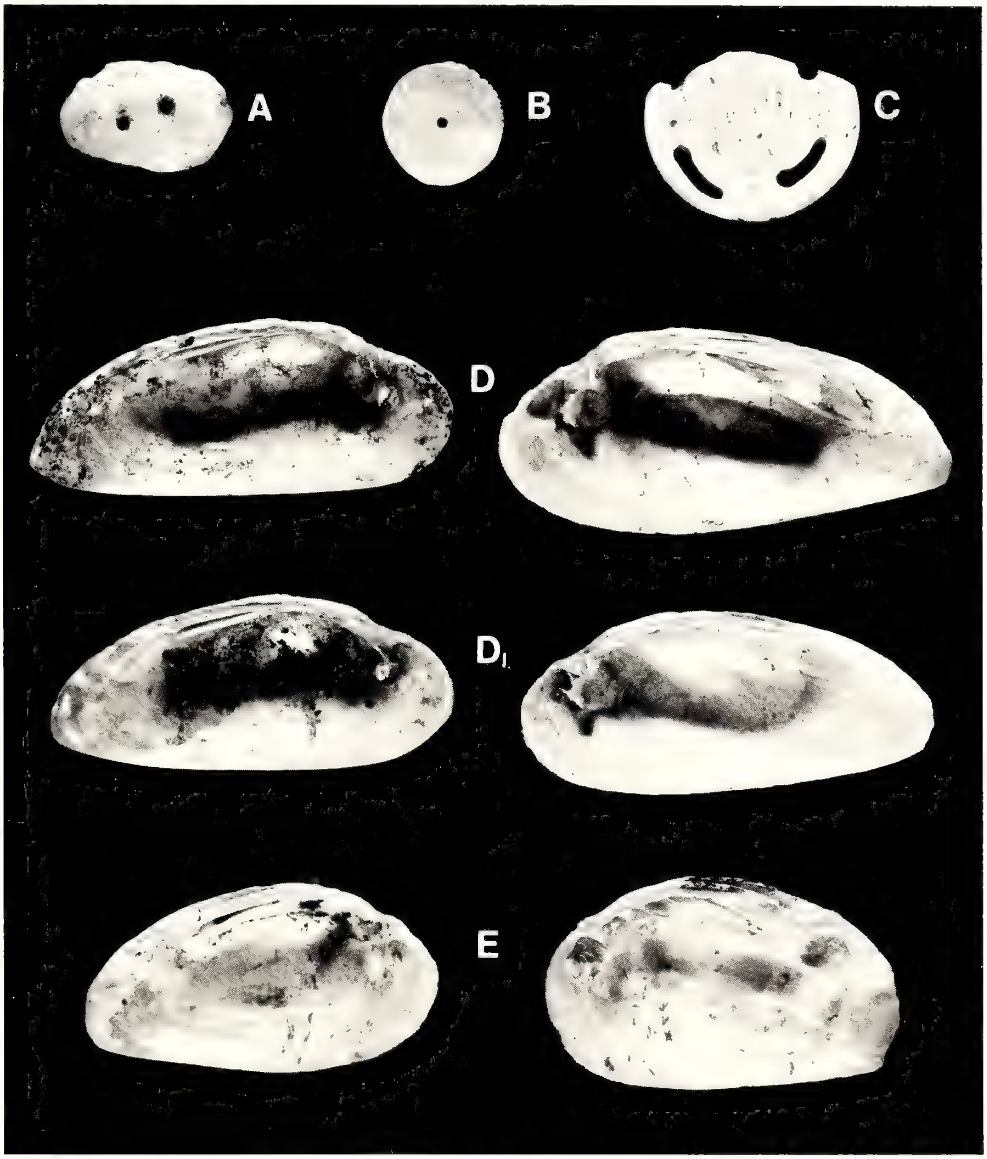

Fig. 3. Modified shells from the McMahan site. Valve section (length, 27.0 mm) with two perforations (A); thin shell disc (diameter, 19.5 mm) with center drilled and partially serrated edge (B); marine shell gorget (diameter, 34.0 mm), rattlesnake design (C); shell scrapers, *Ptychobranchus subtentum* (D, D_1) and *Ptychobranchus fasciolaris* (E).

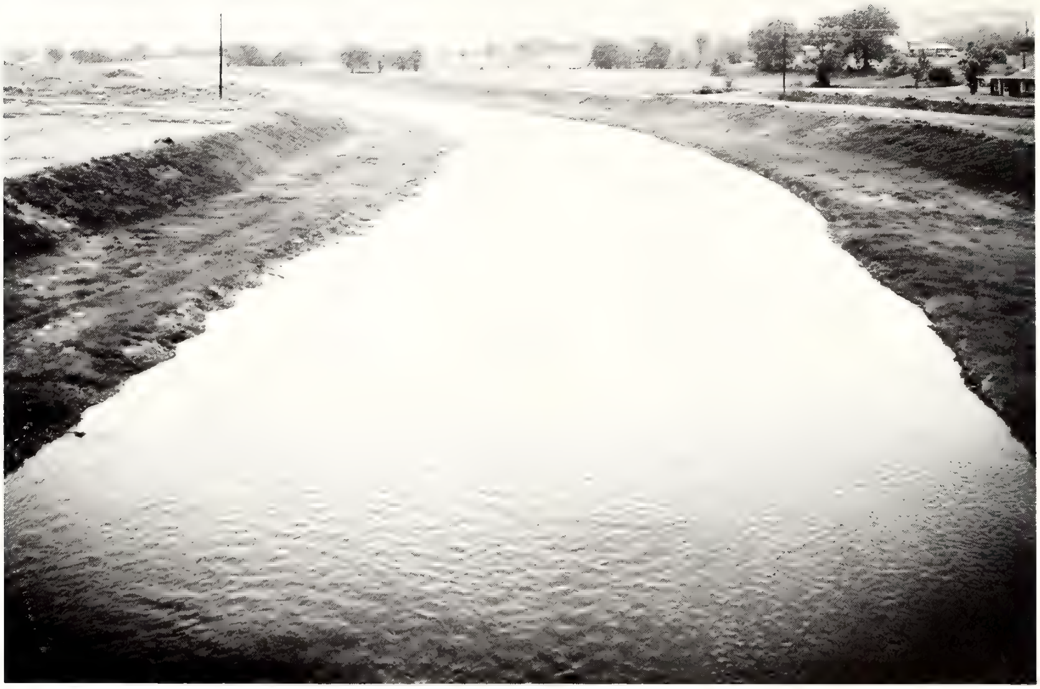

Fig. 4. Widened and relocated channel of West Prong Little Pigeon River, Sevierville, TN, May 1967, looking upstream from U.S. 411 and 441 Highway bridge. McMahan site on left bank beyond bend in the river. Photo courtesy Tennessee Valley Authority.

valves of other species, one specimen of *Elliptio dilatata* and two of *P. fasciolaris*, were encountered that exhibited the ground ventral margin.

PRESENT NAIAD POPULATIONS: THE LITTLE PIGEON RIVER SYSTEM

The Little Pigeon River system flows generally northwest from the Great Smoky Mountains National Park to its confluence with the French Broad River (River Mile 27.4; 43.8 km: Fig. 1), ca. 8.0 km below Douglas Dam. The entire watershed, consisting of 914 km^2, is in Sevier County, TN. Middle Prong and Porters Creek join to form the Little Pigeon River; downstream it is joined by Webb and Bird creeks, East Fork, and Middle Creek and West Prong Little Pigeon River at Sevierville (referred to as West Fork until ca. 1970). Principal tributaries of the West Prong Little Pigeon River are LeConte Creek, Roaring Fork, and Mill and Walden creeks. Total length of the Little Pigeon River is 45.4 km, that of the West Prong Little Pigeon River, 43.0 km. With minor exceptions the upper three-fourths of the drainage system flows in steep, narrow, mountain gorges, heading at elevations up to over 1,830 m at the southern boundary of the Great Smoky Mountains National Park (Tennessee Valley Authority, 1964). With the exception of the East Fork, tributaries of the Little Pigeon and West Prong Little Pigeon rivers are now apparently devoid of mussel populations. In light of the steep gradient, rapid current, and bedrock and boulder substratum characteristic of the majority of smaller streams making up this system, it is doubtful whether viable and varied mussel assemblages ever existed in all but the lower reaches of the Little Pigeon and West Prong Little Pigeon rivers.

Although Sevier County, formed in 1794, is considered predominantly rural, the past three decades have seen a phenomenal growth in urbanization, especially as it relates to the tourist industry. This has come about as the popularity of the Great Smoky Mountains National Park continues to escalate and the cities of Gatlinburg, Pigeon Forge and, to a lesser extent, Sevierville enlarge and diversify their facilities to accommodate the ever-increasing number of tourists. Environmental degradation of the Little Pigeon River system also continues to increase as a result of siltation, discharge from waste water treatment plants, and trash in general. Surprisingly, however, viable populations of several species of endemic fishes, turtles and mollusks continue to survive in very local areas in the lower stretches of the Little Pigeon River, and particularly in the West Prong Little Pigeon River in Sevierville. In the case of freshwater mussels, it seems even more suprising that the greatest diversity of species (albeit not large) and abundance in the Little Pigeon River system can be found in a 1.0 km stretch of the West Prong Little Pigeon River that was widened by the Tennessee Valley Authority during the period from June 1967 to May 1968 (see Figs. 4 and 5). Beginning at the TN Hwy 441 bridge (channel width, 36 m), the width was expanded to 62 m at a point 152 m downstream for a distance of 1.9 km. In addition, the mouth of the river was relocated ca. 0.6 km below its former junction with the Little Pigeon River: this modification eliminated two 180^0 bends and allowed discharge farther downstream, thus eliminating extreme periodic flooding that

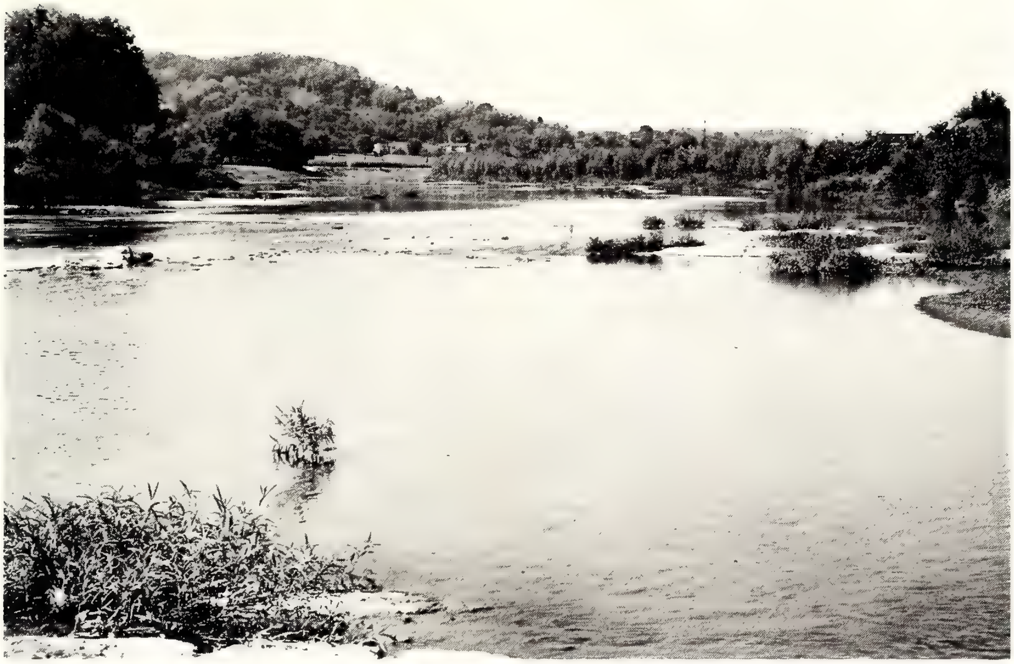

Fig. 5. West Prong Little Pigeon River, looking downstream, during period of low water (July, 1986). McMahan site along right bank.

inundated the main business district and suburbs of Sevierville.

During the period June 1985-May 1987, a total of 15 collecting trips were made in the Little Pigeon River in a stretch from the TN Hwy 66 bridge in Sevierville to just below the confluence with the West Prong Little Pigeon River, a distance of ca. 0.9 km. A total of 118 specimens, representing 11 species, were recovered (Table 3); shells of *Fusconaia barnesiana, Lampsilis fasciola, Villosa vanuxemensis* and *V. iris* comprised 93.2% of the sample. The one individual of *Anodonta grandis* (Say, 1829), the Common Floater, taken here (shell length 85.5 mm) was the only specimen of this species encountered during this study. Except for one individual and a left valve of *Elliptio dilatata* (Rafinesque, 1820), the Spike, found in the West Prong Little Pigeon River, one relic shell (chalky, periostracum badly eroded) recovered in this stretch of the Little Pigeon River was the only other example of this species found in the river system.

Although several locations on the Little Pigeon River from immediately below the confluence with the West Prong Little Pigeon River to its mouth (confluence with the French Broad River), a distance of ca. 7.5 km, were surveyed on six occasions during this two year study, no freshwater mussels were encountered. A substratum of shifting sand, private homes and small businesses lining the east bank and croplands and pastures adjacent to the west bank, plus the last ca. 1.1 km above the mouth being impounded, probably contribute the void in mussel populations. In his study of the effect of rechanneling on the fish population of Middle Creek, Sevierville, Etnier (1972) was of the opinion that substratum instability and the decreased variability of the physical habitat were the most significant factors responsible for changes in the fish fauna. Widening and other modifications of the Little Pigeon River in Sevierville by the TVA, plus the aforementioned conditions downstream, all contributed to reducing the environmental quality of the river for most aquatic organisms. Less than six specimens of *Villosa iris* and *Lampsilis fasciola* were found in the Little Pigeon River at the Walnut Grove Bridge in Sevierville (River Mile 6.7; 10.7 km); these were relic specimens and the apparent paucity of naiads inhabiting this stretch of the river could be due in part to urban development along the banks at this point and upstream. No mussels were found in the Little Pigeon River upstream from the southern city limits of Sevierville, so with the possible exception of an occasional individual becoming established, viable mussel

Table 3. Species of freshwater mussels inhabiting the Little Pigeon River, TN Hwy. 66 bridge to confluence with West Prong Little Pigeon River, Sevier County, TN. Specimens obtained primarily from muskrat feeding stations, June 1985-May 1987.

Species	No. of Specimens	% of Specimens
Fusconaia barnesiana (Lea, 1838)	35	29.41
Pleurobema oviforme (Conrad, 1834)	3	2.52
Anodonta grandis (Say, 1829)	1	.84
Lasmigona costata (Rafinesque, 1820)	1	.84
Toxolasma lividus (Rafinesque, 1831)	2	1.68
Epioblasma capsaeformis (Lea, 1834)	1	.84
Lampsilis fasciola (Rafinesque, 1820)	26	21.85
L. ovata (Say, 1817)	1	.84
Villosa iris (Lea, 1830)	16	13.45
V. vanuxemensis (Lea, 1838)	33	27.73
Totals	119	100.00

populations in the Little Pigeon River are at present restricted to the stretch between the TN Hwy 66 bridge and its confluence with the West Prong Little Pigeon River. A small but apparently stable population of *V. vanuxemensis* was found inhabiting a ca. 0.2 km stretch of the East Fork, but this is apparently the only naiad species living in this small tributary stream.

As previously mentioned (see METHODS), emphasis on surveying the molluscan fauna of the Little Pigeon River system centered on that stretch of the West Prong Little Pigeon River adjacent to the McMahan site. This was started initially after noting a number of shells of endemic species, along with large quantities of shells of *Corbicula fluminea* (Müller, 1774), the Asiatic Clam, scattered along the bottom and at muskrat feeding stations. It was felt that monthly surveys for a period of time (as it turned out, two years) would provide an accurate index to extant species and the relative size of their populations still inhabiting the river, and a comparison of the present mussel assemblage with that from a prehistoric context at the McMahan site.

No quantitative data were obtained for the species of gastropods still inhabiting the Little Pigeon River system. Two species, *Leptoxis praerosa* (most can be referred to the smaller species/form, *L. subglobosa*) and *Pleurocera parvum*, are locally distributed throughout the Little Pigeon River system, including some of the smaller tributaries such as the East Fork, but they appear most abundant in those stretches of the Little Pigeon and West Prong Little Pigeon rivers supporting viable mussel populations. *Io fluvialis, P. canaliculatum* and *Lithasia verrucosa*, taxa represented in the McMahan site molluscan assemblage, have been extirpated from the Little Pigeon River system. *Campeloma* sp. occurs in moderate numbers in the silt/mud substratum in the West Prong Little Pigeon River adjacent to the McMahan site, the only locale where it has been noted. Two other species, *Pseudosuccinea columella* (Say, 1817) and *Physella gyrina* (Say, 1821), have been noted in some numbers under boards and other trash caught in vegetation along the banks; these taxa could be recent, or historic, additions to the molluscan fauna and their numbers could well increase as they appear tolerant of low water quality and a mud/silt substratum.

Table 4 provides a list of the naiad species and the number of each collected in the West Prong Little Pigeon River from June 1985 through May 1987. "Number of Specimens" reflects the quantity of paired valves collected that were judged to be fresh or "recently dead" because they either contained remains of soft parts or the shell had not yet become heavily stained with algae, the periostracum was not eroded (other than normal erosion of the beak), and the nacre was not chalky. The only specimen of *Alasmidonta viridis*, the Slipper Shell, encountered during the two year survey was not included in Table 4 because, although paired, the valves were badly eroded; this individual had probably been dead for several years. The same was true of a right and left valve (two individuals) of *Cyclonaias tuberculata*, the Purple Wartyback; these valves were badly eroded and represent individuals that had died at least several years ago.

Shells of four species, *Fusconaia barnesiana, Lampsilis fasciola, Pleurobema oviforme* and *Villosa iris* comprised nearly 83.0% of all specimens recorded. Specimens of *F. barnesiana*, a locally common species in numerous small streams of the upper Tennessee River drainage, accounted for 45.4% of the present naiad assemblage from the West Prong Little Pigeon River. Prehistorically it appears to have also been a common species in this stretch of the river; 347 valves identified from the McMahan site (9.2%) ranked it as one of the four most numerous taxa in the assemblage. Of the 13 species recorded from the Tellico River by Parmalee and Klippel (1984), shells of *F. barnesiana* amounted to 9.1% of the total. *P. oviforme*, another locally common shell in small- to medium-sized rivers, totaled 8.8% and 8.7% respectively in the Tellico and West Prong Little Pigeon river mussel assemblages. Both *V. iris* and *V. vanuxemensis* exhibit viable populations in the West Prong Little Pigeon and Little Pigeon rivers, but the number of individuals from the West Prong accounted for only 8.7% of the total number of specimens while those from the Little Pigeon River amounted to 41.5%. *V. vanuxemensis* is a species adaptable to medium-sized rivers as well as small tributary and headwater streams, and one that often becomes locally abundant; 48.2% of the mussels (543 specimens) obtained by Parmalee and Klippel (1984) from the Tellico River were this species.

Table 4. Species of freshwater mussels inhabiting the West Prong Little Pigeon River, Sevier County, Tennessee. Specimens obtained primarily from muskrat feeding stations, June 1985-May 1987.

Species	No. of Specimens	% of Specimens
Fusconaia barnesiana (Lea, 1838)	689	45.39
Quadrula pustulosa (Lea, 1831)	2	.13
Elliptio crassidens (Lamarck, 1819)	1	.06
E. dilatata (Rafinesque, 1820)	1	.06
Pleurobema oviforme (Conrad, 1834)	132	8.69
Lasmigona costata (Rafinesque, 1820)	47	3.10
Toxolasma lividus (Rafinesque, 1831)	50	3.29
Epioblasma capsaeformis (Lea, 1834)	46	3.03
Lampsilis fasciola (Rafinesque, 1820)	330	21.74
L. ovata (Say, 1817)	53	3.49
Leptodea fragilis (Rafinesque, 1820)	1	.06
Medionidus conradicus (Lea, 1834)	12	.79
Potamilus alatus (Say, 1817)	21	1.38
Villosa iris (Lea, 1830)	103	6.78
V. vanuxemensis (Lea, 1838)	30	1.98
Totals	1,518	99.97

One of the most numerous of the naiad species inhabiting both the Little Pigeon and West Prong Little Pigeon rivers is *Lampsilis fasciola*; individuals collected from both rivers over the two year survey period accounted for approximately 22.0% of all specimens in each. Nearly 10.0% of the valves recovered from the McMahan site were those of this species. At least five other taxa, *Potamilus alatus, Lasmigona costata, Lampsilis ovata, Epioblasma capsaeformis,* and *Medionidus conradicus* appear to be maintaining viable populations in the West Prong Little Pigeon River, although the latter species is rare. Of special interest is the occasional establishment of an individual of a species generally associated in the Mississippi or Interior Basin drainage: these include *Quadrula pustulosa* (2 juvenile specimens, ca. 5 and 6 years of age, plus 2 relic right valves); *Elliptio crassidens* (1 living adult, 2 relic pairs and 1 relic left valve); *E. dilatata* (1 specimen, 1 left valve); *Leptodea fragilis* (1 specimen: shell length 88.5 mm; left valve of a juvenile: shell length 43.4 mm). Probably included in this category is *Cyclonaias tuberculata*, based on the relic right and left valves previously mentioned. Very possibly migratory host fishes, moving up the Little Pigeon River from the French Broad River, provide the mechanism for this dispersal. Thus far their numbers have not become great enough to result in the establishment of viable populations. Of the living taxa of freshwater mussels reported here from the Little Pigeon River system, *L. fragilis* is the only species that was not represented in the archaeological assemblage from the McMahan site.

SUMMARY

The prehistoric molluscan fauna of the West Prong Little Pigeon River, Sevier County, Tennessee is one of the richest and most diverse known for a small river in the upper Tennessee River drainage. Archaeological salvage excavations carried out periodically from June through December 1985 at the McMahan site, a late Mississippian (AD 1300-1600) village and mound complex situated adjacent to the West Prong Little Pigeon River, resulted in the recovery of ca. 7,400 identified aquatic gastropod shells (6 taxa) and 3,855 freshwater mussel valves (45 taxa). Shells of *Leptoxis praerosa* and *Pleurocera parvum* composed 93% of the gastropod specimens recovered. The naiad assemblage was dominated by *Fusconaia barnesiana, F. subrotunda, Lampsilis fasciola, Villosa* spp. and *Ptychobranchus subtentum* (ca. 65% of all identified valves). Although several taxa represented in the archaeological sample, e.g. *F. subrotunda, Elliptio crassidens, Cyclonaias tuberculata, Pleurobema cordatum*, and *Dromus dromas* can inhabit the deep water of large rivers as well as shallow small rivers (in some instances reflected by differences in shell form), all species identified from the McMahan site are known to occur in small- to medium-sized rivers. However, approximately 30 of these reach their widest distribution and greatest population densities in small- to medium-sized rivers with normal depths of 1 m, a coarse gravel/small cobble/sand substratum, riffles and swift current.

Ortmann (1925) concluded "...that originally there must have existed a separation of two faunistic types in two different drainage systems, a Cumberlandian River and an Interior Basin River, and that subsequently these two systems became connected, so that their faunas had a chance to mingle." He noted earlier (Ortmann, 1924) that "At the present time, the distribution of the Cumberlandian Naiad fauna is markedly discontinuous, being found in the upper Cumberland, the upper Duck, and the Tennessee above the Mussel Shoals, but not in the lower Cumberland, the lower Duck, and probably also the lower Tennessee (downward from some point below the Mussel Shoals, which has not yet been ascertained)." Of those species whose origin has been determined with some degree of certainty (e.g. Ortmann, 1925; van der Schalie, 1973), the naiad taxa represented at the McMahan site consist of about 43% from the Interior Basin (Mississippian) drainage and 57% from the Cumberlandian region (see Table 2). Former stretches of pool and riffle habitat in the West Prong Little Pigeon River within close proximity of the McMahan site apparently provided ideal conditions for the establishment of an abundant and varied molluscan fauna. Naiad taxa whose origin was the Interior Basin drainage reached the Little Pigeon River system via the French Broad River.

Analyses of a sample of substratum taken from a stretch of the West Prong Little Pigeon River that appeared to provide the best mussel habitat, judging by the number of live individuals and taxa observed during periods of low summer water levels, was composed of the following particle sizes (after Wentworth, 1922): medium sand, 16.34%; coarse sand, 66.87%; very coarse sand, 13.48%. The balance was composed of small pebbles, granules, fine sand and very fine sand. This type of substratum, whether in large uniform expanses, e.g. 30 x 90 m^2, or in small patches among large cobbles or between layers of bedrock, provides the most suitable habitat for present day molluscan populations. A river habitat (Fig. 2) probably not unlike the present one adjacent to the McMahan site, clear cut banks and channel widening by TVA notwithstanding, existed in late prehistoric times and supported a rich molluscan fauna that was heavily exploited by the Indian.

Data on species distribution and population densities of freshwater mussels inhabiting the Little Pigeon River system were obtained from June 1985 through May 1987. The primary source of quantitative data was obtained from shells discarded by muskrats at feeding stations. Although the Little Pigeon River and several tributaries that could have supported mussel populations were surveyed, emphasis was placed on a ca. 1.0 km stretch of the West Prong Little Pigeon River adjacent to the McMahan site. In spite of, or as a result of a widening and straightening of the channel by TVA in 1966-1967, viable mussel populations of 11 species of mussels still exist in this stretch in spite of continued severe degradation of the river environment. Occasionally individuals of other naiad species (in this study, five taxa) become established in the Little Pigeon and West Prong Little Pigeon rivers, but apparently in such low numbers that viable populations are unable to develop.

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EVALUATION OF TECHNIQUES FOR AGE DETERMINATION OF FRESHWATER MUSSELS (UNIONIDAE)

RICHARD J. NEVES
AND
STEVEN N. MOYER[1]
VIRGINIA COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT
DEPARTMENT OF FISHERIES AND WILDLIFE SCIENCES
VIRGINIA POLYTECHNIC INSTITUTE AND STATE UNIVERSITY
BLACKSBURG, VIRGINIA 24061, U. S. A.

ABSTRACT

Age validation and an assessment of four age determination techniques; shell ashing, thin-sectioning, acetate peels, and enumeration of external growth bands, were conducted on several species of freshwater mussels (Unionidae) in southwestern Virginia. The recovery of tagged and marked specimens of four species after one to three years confirmed the formation of one distinct annulus per year on and in shells. Thin-sectioning of valves was the most effective technique for aging and provided a high degree of both accuracy and precision. Shell ashing was totally unreliable, and acetate peels were inferior to thin-sections. The commonly used method of counting external growth bands on shells consistently underestimated the ages of older specimens and is of limited use in age determination of unionids.

The determination of absolute ages of bivalves is essential to derive population statistics for managing their harvest and conservation. Shells (valves) of freshwater mussels (Unionidae) exhibit pronounced bands or rings on their external surface, and the distance between bands decreases progressively with an increase in shell size. The significance of these bands and their use to derive absolute ages of mussels was discussed by early researchers (LeFevre and Curtis, 1912; Isley, 1914; Coker *et al.*, 1921). Based on the cyclical periodicity of band formation on valves, ages of freshwater mussels have been determined using the techniques of enumerating growth rings on the valve surface (Chamberlain, 1931; Stansbery, 1961), and ashing shells in a muffle furnace to separate the bands (Sterrett and Saville, 1975). The occurrence of growth bands within radial cross-sections of the shell and hinge ligament has provided an additional means of age determination (Hendelberg, 1960; Bjork, 1962; Ray, 1978; McCuaig and Green, 1983).

In most early attempts to age unionids, investigators relied on the visibility of growth bands on the outer surface of shells. Although these bands can be used to delimit age of some species, in other species subjective and conflicting ages typically result. Growth bands on lentic species, which grow rapidly early in life, are characterized by regular spacing and distinctness (Chamberlain, 1931; Stansbery, 1961), whereas those on stream-dwelling mussels are less pronounced (Grier, 1922; Brown *et al.*, 1938). Investigations to determine age from external growth bands of riverine mussels, hereafter called the growth ring method, is often hampered by erosion of the shell surface, obscurity of bands on dark-colored valves, subjectivity in distinguishing annuli from stress-produced checks, and the inability to count closely deposited bands near the valve margin of older specimens (Ansell, 1968; Coon *et al.*, 1977; Lutz and Rhoads, 1980). Population statistics derived from this method, which apparently lacks both accuracy and precision, are therefore fraught with problems.

In contrast to the growth ring method most often used on freshwater bivalves, the techniques for determining ages of marine bivalves have been rigorously tested and are apparently more reliable. Most age studies of marine bivalves since Barker (1964) have used two sectioning techniques, thin-sections or acetate peels, to determine absolute ages; these methods are now used routinely in marine malacology (Clark, 1980). Both the chondrophore and entire valve of marine clams have proven to be useful for age determinations (Ropes and O'Brien, 1980), and detailed descriptions of the methods are provided by Lutz and Rhoads (1980) and Ropes (1984).

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[1] Present address: National Wildlife Federation, 1412 16th Street, N.W., Washington, D.C. 20036, U.S.A.

The annual formation of winter growth bands on the valve surface of some freshwater mussel species has been documented (Isley, 1914; Chamberlain, 1931; Negus, 1966; Haukioja and Hakala, 1978), but the formation of internal annuli lacks appropriate verification. Most studies that have estimated ages of mussels by these various methods typically omit age validation (i.e. proof of the accuracy of the technique). Validation of these methods for mussels is necessary because of the presence of less prominent, stress-related growth checks in bivalve shells, termed pseudoannuli or "false" annuli. Some researchers have been able to distinguish the difference between annuli and "false" annuli with relative ease (Chamberlain, 1931; Negus, 1966; Day, 1984); others have had difficulty, especially with riverine species (Coon *et al.*, 1977; Haukioja and Hakala, 1978). Previous studies with unionids in the upper Tennessee River drainage, of Virginia and Tennessee, have also experienced difficulty in delimiting annuli and recognized the need for validation (Zale, 1980; Weaver, 1981). Age validation is an essential prerequisite for obtaining sound population statistics, and the application of routine but unvalidated methods to all species can result in significant misinterpretations of biological data (Beamish and McFarlane, 1983a, 1983b).

The three objectives of our study were: (1) validation of the annual formation of growth bands on and in the valves of various sizes and species of unionid mussels; (2) tests of the utility of shell ashing, thin-sectioning, and acetate peels for freshwater mussels; (3) comparison of the ages of specimens derived from the growth ring and thin-sectioning methods.

MATERIALS AND METHODS

ANNULUS VARIATION

A mark and recovery program was conducted from 1979 to 1983 to validate the annual deposition of growth bands, to determine the season of annulus formation, and to provide empirical data on mussel growth. Four relatively common mussel species, representing three subfamilies of unionids, were selected for this phase of the study: *Pleurobema oviforme* (Conrad, 1834); *Lasmigona subviridis* (Conrad, 1835); *Villosa vanuxemi* (Lea, 1838); and *Medionidus conradicus* (Lea, 1834). Specimens were obtained from three sites in western Virginia: New River, Montgomery County; North Fork Holston River, Smyth County; Big Moccasin Creek, Russell County. A total of 1452 adult mussels were collected by hand, transported to our laboratory, and held in a 300 *l* aerated, recirculating tank (Table 1). Each specimen was measured (length and height) with calipers to the nearest 0.1 mm and marked by one of three methods, numbered tag only, tag plus valve notch, and tag plus painted valve. These marking methods were used to record shell growth for a known time period and to recognize differences between annuli and other bands (false annuli) formed externally and internally on the valves.

One valve of each mussel was tagged with a 3 x 5 mm fluorescent orange, sequentially numbered disc tag (Floy Tag Company, Seattle, Washington), held in place by Duro superglue (Loctite Corporation, Cleveland, Ohio). A small triangular notch was filed in the ventral margin of notched specimens, and red fingernail polish was applied to the shell margins of painted specimens. The marked specimens were transplanted to two sites (I and II) in each stream; specimens at site I (15 to 25 m^2 in area) were tagged and 7% were painted, and those at site II (0.7 to 3 m^2) were tagged and notched (Table 1). Mussels were returned to their collection sites within 2 weeks and placed, properly oriented, in the substratrum. At site I in the New River, 150 tagged mussels were divided among three substrata-filled chicken wire enclosures (13 mm mesh; 76 x 76 x 13 cm) set into the substratrum to inhibit mussel dispersal and facilitate periodic examination. The remaining mussels at this site were placed near the enclosures. Sites in all three streams were identified either by landmarks, streambed features, or markers.

In each stream, mussels at site I were recovered after 1 year for annulus validation, and a sample of about 12 mussels at site II was collected quarterly during the first year for examination of seasonality in growth band deposition. Some specimens that could not be found 1 year after planting were collected up to 4 years later (1983). Recovered mussels were sacrificed, and incremental growth on valves was measured and examined for annulus formation externally and internally, under a dissecting microscope.

EVALUATION OF AGE TECHNIQUES

Ashing of shells to separate growth layers followed procedures similar to those used by Sterrett and Saville (1974). Initial cuts made on a Buehler Isomet low-speed saw unit with a diamond-impregnated blade (Buehler Ltd., Evanston, Illinois) were: (1) from the umbo to the shell margin along the vector of maximum length, and (2) from the umbo to the shell margin perpendicular to the first cut. The triangular wedges of shell produced by these cuts, with sectioned surface exposed on two sides, were ashed in a muffle furnace. Sterrett and Saville (1974) recommended ashing at either 500°C for 10 minutes or 600°C for 5 minutes. Because temperature and time are the factors apparently crucial for producing good results, a size range of shells (20-80 mm) was ashed at both of the recommended times and temperatures. However, the resulting ashed shells were too brittle to allow effective separation of many of the growth layers. Therefore, we conducted a series of ashing time and temperature trials to evaluate the utility of this technique: 300°C for 1, 5, 10, 15, or 20 min; 400°C for 1, 5, 10, or 15 min; 500°C for 1, 5, or 10 min; and 600°C for 1 or 5 min. Preliminary ashing tests indicated that each of these combinations of times and temperatures could produce usable results. Three shells, small (<40 mm), medium (40-60 mm), and large (>60 mm), were ashed in each of the 14 trials. All trials were later replicated to corroborate initial results. Utility of the shell ashing technique was assessed by (1) how well annual layers could be separated, and (2) how well growth bands could be distinguished externally and in cross-section.

Thin-sectioning of valves followed procedures similar to those described by Clark (1980), in which a low speed saw unit and diamond-impregnated blade was used. An initial

Table 1. Number of mussels of four species tagged in 1979 - 1982 at two sites each on Big Moccasin Creek (BMC), North Fork Holston River (NFHR), and New River (NR), western Virginia.

Stream, Site and Date	*Pleurobema oviforme*	*Medionidus conradicus*	*Villosa vanuxemi*	*Lasmigona subviridis*	Total
BMC I					
Oct 1979	—	63	29	—	92
Oct 1980	39	2	6	—	47
Sept 1981	101	165	103	—	369
BMC II					
Jul 1982	2	35	12	—	49
NFHR I					
Sept 1981	152	139	108	—	399
NFHR II					
Jul 1982	30	27	41	—	98
NR I					
Apr 1982	—	—	—	320	320
NR II					
Jul 1982	—	—	—	78	78
Total	324	431	299	398	1452

cross-sectional cut from the umbo to the shell margin followed the vector of maximum growth (posterio-ventrally), since it generally intersected growth lines at right angles. Shell cuts were then bonded to petrographic micro-slides (27 x 46 mm) with epoxy glue (Buehler epo-kwick) and vacuum-sealed into a petrographic chuck attached to the cutting arm of the saw. Because the thickness of the second cut was critical to producing thin-sections of suitable quality, several cuts ranging from 200 to 380 μm were made to determine optimal thickness for growth band detection. A thickness of 280 μm was considered to be best for consistent, high resolution thin-sections and was used in all subsequent sectioning of valves.

The utility of thin-sectioning was evaluated on a variety of mussel species from rivers in southwestern Virginia. Shell lengths ranged from 15 mm for *Medionidus conradicus* to 210 mm for *Potamilus alatus* (Say, 1817), although most shells were 20 to 80 mm long. Shells longer than 60 mm had to be cut more than once because the saw blade was only 114 m in diameter. The final cut through the umbonal region of large shells included all internal growth lines. Sectioned shells and derived thin-sections were examined under 4X magnification, and felt-tip pen marks were made adjacent to the point where each growth line exited at the shell surface. The cross-sectioned shell was then superimposed on the marked thin-sections. This justaposition of shells allowed for visual comparison of internal with external growth lines to corroborate contiguity and to identify false annuli on the valves.

Acetate peels from sectioned shells followed the method of Kennish *et al.* (1980). Shells of *Pleurobema oviforme, Medionidus conradicus, Villosa vanuxemi,* as well as *Fusconaia cor* (Conrad, 1834) and *F. cuneolus* (Lea, 1840), two federally endangered species, were separated into small (< 40 mm), medium (40-60 mm), and large size groups (> 60 mm). An initial cross-sectional cut was made with the low-speed saw from the umbo to the shell margin along the vector of maximum growth. Although Kennish *et al.* (1980) suggested pre-embedding the valves in an epoxy resin first to prevent fracturing during sectioning, the stability of the low-speed saw allowed sectioning of most shells without fracture (Clark, 1980). Valve sections were then ground by hand on sequentially finer grit sizes: 320, 400, and 600 (Buehler carborundum grits) and polished with polishing alumina (Fisher Scientific Co., Fairlawn, New Jersey) on felt polishing cloth. Because acid-etching is the critical step in this technique and is apparently related to shell structure, mineralogy, organic content, and state of preservation (Kennish *et al.*, 1980), etching times and HCl concentrations are expected to differ slightly among species. Therefore, polished sections of each species and size group were etched in a dilute solution of HCl at various concentrations (1%, 5%, 10%) and time periods (15 sec to 5 min). This allowed development of an optimal procedure for shells of a given size and species. One valve was used in each of the etching time and HCl concentration trials. The etched shell sections were washed under running water and dried.

In the last step of the peel process, we placed the etched section firmly on a strip of acetate (2 mm thick) covered with acetone, and pressed for 30 sec. After the acetone dried completely (2-3 hr), the valve was pulled from the acetate strip, leaving an imprint (the peel) on the acetate. Internal growth bands on the peel were counted under 4 to 10X magnification. Quality of the acetate peels was judged by two criteria: clarity of growth bands in the umbonal region, and degree to which bands could be traced from the umbo to the shell margin.

COMPARISON OF EXTERNAL AND INTERNAL AGES

The valves of 82 specimens of *Fusconaia cor* and *Pleurobema oviforme* were selected for this comparison.

These species had relatively distinct external growth bands and were aged by the growth ring method. Later, the same valves were thin-sectioned, as previously described. Ages determined by these two methods were plotted graphically, and a Wilcoxon signed rank test was used to compare differences.

RESULTS

ANNULUS VALIDATION

A total of 521 (36%) of the 1452 marked mussels was recovered from the three streams (Table 2). Recovery rates of specimens from Big Moccasin Creek and the North Fork Holston River were similar, 49.1 and 47.1% respectively; the largest species, *Pleurobema oviforme*, was the most frequently recovered. Both sites on the New River yielded low returns (3.2%) because of specific problems. Muskrats (*Ondatra zibethicus* L. along the New River removed 55 marked specimens (found in shell middens) in June-July 1982, and one enclosure of 50 mussels was vandalized in October. In addition, a thick mat of *Elodea* developed by fall 1982 and summer 1983, and caused considerable siltation and mortality of marked mussels.

Table 2. Recovery and validation of annulus formation on mussels marked in Big Moccasin Creek (BMC), North Fork Holston River (NFHR), and New River (NR), western Virginia.

Stream/Species	Mussels Recovered No.	Mussels Recovered %	No. validated
Big Moccasin Creek			
Pleurobema oviforme	83	58	7
Medionidus conradicus	101	38	10
Villosa vanuxemi	90	60	9
Subtotal	274	49	26
North Fork Holston River			
P. oviforme	109	60	4
M. conradicus	63	38	9
V. vanuxemi	62	42	20
Subtotal	234	47	33
New River			
Lasmigona subviridis	13	3	4
Total	521		63

Of the three marking methods tested, notching of valves was the most useful for recording shell growth and annulus deposition. Annuli appeared as dark bands in sectioned valves (Clark, 1974; Lutz and Rhoads, 1980), and were evident on 25 (27%) of the 94 notched specimens recovered at site II in the streams. Notching readily identified the origin of incremental growth and subsequent growth at the shell margin (Fig. 1). Thin-sections through the notch clearly delineated incremental growth and the presence of a growth band. An annulus was validated on all notched shells that grew more than 1 mm/yr and on several shells that grew 0.5 to 1.0 mm/yr. Several specimens, marked between 1979 and 1982 and collected in 1983, showed one annulus for each year at large.

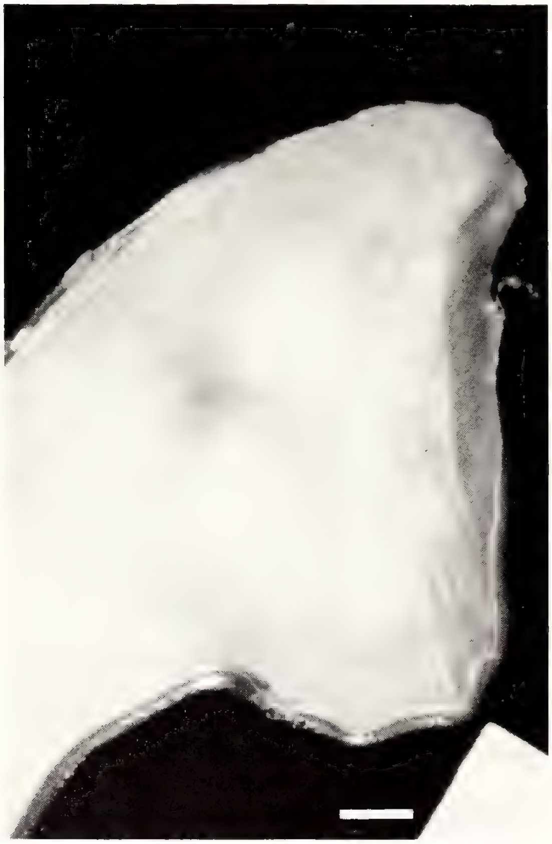

Fig. 1. Thin-section of the umbonal region of *Pleurobema oviforme* showing internal growth lines (bar = 1 mm).

Although the disc tags remained firmly attached to all specimens upon recovery, mussels with only tags were less useful for documenting growth bands. Only 38 (9%) of 425 recovered specimens from site I in the streams were useful for annulus validation. All mussels that grew more than 1.5 mm/yr were validated, but lack of precision with caliper measurements and a fragile shell margin prevented annulus validation on a higher percentage of the slower-growing specimens. Fingernail polish on shell margins was completely ineffective. Within 3 months after marking, it had sloughed from the shells apparently due to abrasion in the substratum.

Annulus formation was documented on 63 (12%) of the 521 specimens recovered from all sites (Table 2). Although this percentage appears low, only specimens with readily measurable incremental growth in length (1.0-1.5 mm, depending on marking method and species) could be used for validation. Occurrence of single (annual) growth bands was confirmed in the shells of all four marked species. Because 83% of the recovered specimens grew less than 1 mm, growth bands formed during the last year on these mussels were nearly indistinguishable from those formed during the penultimate year (Table 3). Growth was most rapid in *Lasmigona subviridis*, the most thin-shelled species, whereas

Table 3. Annual growth increments on mussels tagged and recovered in Big Moccasin Creek, North Fork Holston River, and New River, western Virginia.

Stream and Species	Annual increment (mm)									
	(0-<1)		(1-<2)		(2-<3)		(3-<4)		(4-<5)	
	No.	%	No.	%	No.	%	No.	%	No.	%
Big Moccasin Creek										
Pleurobema oviforme	67	81	12	15	2	2	1	1	1	1
Medionidus conradicus	92	91	6	6	2	3	—	—	—	
Villosa vanuxemi	71	79	18	20	1	1	—	—	—	—
North Fork Holston River										
P. oviforme	98	90	11	10	—	—	—	—	—	—
M. conradicus	61	97	2	3	—	—	—	—	—	—
V. vanuxemi	51	82	11	18	—	—	—	—	—	—
New River										
Lasmigona subviridis	42	57	20	27	9	13	2	2	1	1
Total	482	83	80	13	14	3	3	<1	2	<1

adults of the other species grew more slowly.

Despite the slow growth of most of the recovered mussels, validation results provided convincing evidence of the formation of a single growth band each year. An annulus was formed in all tagged specimens that grew more than 1.5 mm and all tagged and notched specimens that grew more than 1.0 mm during the year. None of these lacked an annulus, nor had they more than one prominent growth band.

Only limited evidence was obtained on the seasonality of annulus formation, primarily because growth was slow throughout the year. Some specimens from the three streams provided evidence that the growth band had formed between January and May. No annulus was observed on specimens examined during fall and winter, but valves of four mussels examined in May and all of 16 valves examined in July had an annulus within the outer layer of incremental growth. Although sample sizes are small, it appears that the annulus is formed (becomes visible) in spring in western Virginia.

EVALUATION OF AGE TECHNIQUES

All ashing trials failed to meet our two criteria for suitability in age determination; i.e. separation of each annulus and recognition of growth bands externally and internally. Shells were either too brittle or inseparable at many annuli after the tests. Most shells ashed at 400°C for 10 and 15 min did separate along the first one to four annual growth bands. However, subsequent annuli could not be separated consistently; shells were brittle and crumbled when manipulated. Ashing also tended to obliterate the recognition of growth bands, making true annuli and false annuli indistinguishable.

The acetate peel technique was less effective than thin-sectioning, both in terms of clarity of growth bands in the umbo region and degree to which bands could be traced throughout the shell. Because of the similarity of the thin-section and peel techniques, and higher resolution produced by thin-sectioning, acetate peels produced by the method described were judged to be inferior to thin-sections for determining ages of mussel shells.

Thin-sectioning of valves was the most effective technique and usually provided a high degree of precision (Fig. 1). A section thickness of 280 μm produced consistent, high quality preparations for valves of all species over a wide range of shell lengths (15-210 mm). Ages of sectioned shells ranged from 3 to 56 years. The clarity of thin-sections resulted in a high degree of accuracy because the contrast between true annuli and false annuli was pronounced, and annuli could usually be traced continuously from the umbo to the shell margin. The entire sectioning procedure required 0.5 to 1 hour per valve (excluding overnight hardening of the epoxy glue), depending on shell size and thickness.

RECOGNITION OF ANNULI

Species that displayed distinct external annuli also had distinct internal annuli. Shells of *Pleurobema oviforme* and *Fusconaia cor* typically had well-defined internal and external annuli, unlike those of *F. cuneolus, Medionidus conradicus* and *Lasmigona subviridis.* Internal annuli of *Villosa vanuxemi* were readily distinguished, but the external growth bands were obscured by the dark periostracum of this species. Significant variability in the clarity of external annuli was also evident within a species; erosion of the shell surface was the major contributing factor, and this problem was directly correlated with age. Young specimens (3-6 yrs) were rarely affected, but in older individuals (7-15 yrs), the first and often second annulus was eroded. The first two annuli were typically missing in the oldest specimens (>15 yrs), and those older than 20 years could not be aged externally because the periostracum had become extensively damaged. Shell corrosion (dissolution) was also evident on shells from all three streams. Prior dissolution of calcium carbonate in the umbonal region apparently resulted in pit formation.

False annuli occurred occasionally in all species examined. Thin-sectioning provided the best method for identifying false annuli because true annuli could be traced from umbo to shell margin. In contrast, false annuli were characterized by an incomplete growth line in thin sections (Fig. 2). Recognition of false annuli was much more difficult

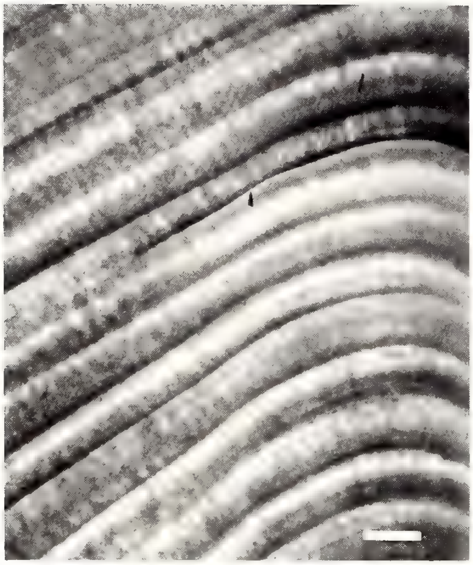

Fig. 2. Thin-section of a valve of *Pleurobema oviforme* with a false annulus (arrow) among true annuli (bar = 0.5 mm).

on the shell surface. For example, the inclusion of small particles from the substratum into shells often caused the formation of a false annulus. This false growth check was observed most commonly in shells of females, particularly in *Villosa vanuxemi* from Big Moccasin Creek and the North Fork Holston River. Incorporation of these particles in the shell produced a thick, dark line both internally and externally on the shell (Fig. 3). This growth check appeared to be a true annulus on the shell surface, but was not continuous in the cross-sectioned shell.

EXTERNAL VERSUS INTERNAL AGES

Growth bands on the external surface of valves of *Pleurobema oviforme* and *Fusconaia cor* were readily visible and were more distinct than those in most other species available for such a comparison. Annuli were easily discerned on specimens 3 to 8 years old, but became more tightly grouped and less distinct on valves of mussels 8 to 15 years old. Shells of mussels more than 15 years old were difficult to age because surface annuli were nearly contiguous or indistinguishable even under magnification. If the periostracum was damaged by erosion or corrosion on older specimens, frequently no age estimates were possible. Erosion of valves was especially prevalent on old specimens of *P. oviforme.* No valves older than 20 years, as determined by the thin-section method, could be aged by the growth ring method because of periostracum damage. Erosion was also the probable cause for loss of the first and often second annulus on some valves older than age 6 years. The thin, organic-rich growth checks apparently were less solid than the calcium carbonate deposition in annual growth, and shell fractures in young specimens were occasionally evident along the annulus. However, cleavage lines were nearly always visible on the shell and were counted as annuli.

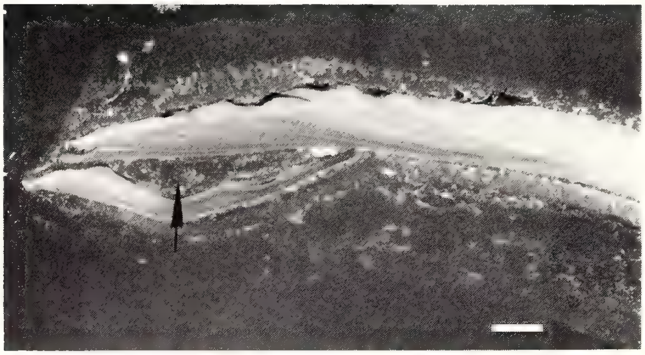

Fig. 3. Thin-section of a valve of *Villosa vanuxemi* with the incorporation of sediment (arrow) into the valve (bar = 1 mm).

A comparison of ages derived by counts of external annuli and by thin sectioning on 82 specimens of *Fusconaia cor* and 49 *Pleurobema oviforme* indicated that counts of external annuli consistently yielded underestimates of ages (Fig. 4). Differences in ages determined by the two methods were highly significant ($P < 0.01$). The degree of underestimation was directly proportional to age estimates; the older the specimen, the greater the underestimate of age by the growth ring method. The two methods yielded similar ages for *F. cor* up to age 10, but mussels 11 to 25 years old were underestimated by 1 to 5 years when external annuli were counted. Thin-sectioning was more effective, particularly on old specimens (>20 yr). Eight valves of *P. oviforme* older than 20 years could not be aged externally due to periostracum damage; these specimens ranged in age from 25 to 56 years based on thin-sections.

On thin-sections of the latter two species, marks were made adjacent to the exit location of each annulus at the shell margin to allow visual comparisons with cross-sectioned shells from which the thin-sections were cut. Comparison of the two clearly corroborated the occurrence of one externally visible annulus with its internal counterpart in every shell. This external-internal comparison also demonstrated the occasional presence of thinner, false annuli on the shell surface that had no counterpart internally. Generally, internal annuli were much easier to distinguish than external annuli, especially near the shell margin of older specimens.

DISCUSSION

Deposition of one prominent growth band annually was validated in 12% of the tagged specimens that were recovered from the three study streams. The relatively low recovery rate (36%) and slow growth (<1 mm) of most specimens limited the availability of a larger sample size. Negus (1966) recovered only 56 (9.7%) of 572 marked specimens of three freshwater mussel species in the Thames River, England after 1 year to validate annulus formation; of these, 43 (77%) showed an annulus. Although recovery rates of marked bivalves have been typically low in both freshwater and marine environments (Murawski *et al.*, 1982; Schaul and Goodwin, 1982), formation of annual growth bands in bivalves from temperate climates appears to be common. In the tropics, unionids also

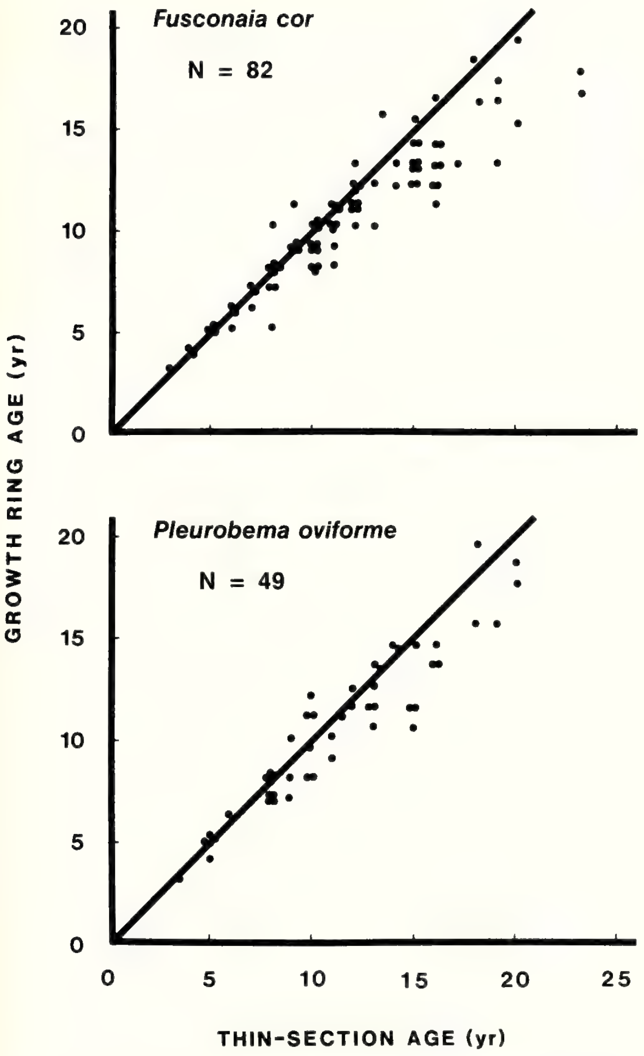

Fig. 4. A comparison of age estimates for two species aged by the thin-sectioning and external growth ring methods. Data points below the 45° line represent underestimates of specimen ages by the growth ring method.

exhibit shell bands, but the causes for their formation are probably different from those for temperate species (McMichael, 1952). This apparent regularity in banding could lead some investigators to assume that annulus formation is a universal phenomenon and that age validation might not be necessary. However, we caution that annual periodicity of growth line deposition is a hypothesis that should be confirmed for each species and locality before it is accepted.

The slow growth of most tagged specimens (96% grew less than 2 mm per year) was the major handicap in age validation. Growth increments along the shell margin of these specimens were insufficient to allow clear separation of growth during the year after tagging from growth in the penultimate year. Ages of most of the tagged specimens, determined later by thin-sections, were 8 to 20 years. These older, larger specimens proved to be unsuitable, in retrospect, for this component of the study. Our age validation efforts were most successful with mussels of the relatively faster growing, younger age-classes. Therefore, a range of size classes of sufficient number should be used in age validation to overcome the difficulties posed by the slow growth of adults of riverine species.

Other problems associated with slow growth included accuracy of caliper measurements and growth layer detachment. Unnotched mussels that grew less than 1 mm per year had to be excluded because rough shell margins contributed to measurement error with calipers, and annulus deposition could not be confidently ascertained. The narrow growth band along the shell margin often became brittle after the specimens were killed and occasionally broke during measurement or thin-sectioning. Despite these problems with age validation, successes and failures provided experience that improved precision in age determinations of shells. For shells that grew sufficiently for measurement during the 1 year period, the formation of a single growth band per year was confirmed. The identification of both internal and external growth bands for a specimen facilitated the recognition of true versus false annuli and contributed to our confidence in age determinations.

As judged by counts of annuli on mussel shells and growth measured for up to 4 years at study sites, adults of riverine species in Virginia grow slowly and reach maximum ages greater than those reported for lentic species (Grier, 1938; Stansbery, 1961). Longevities of the species aged by thin-sections ranged from 22 to 56 years. These ages exceed those reported for some species in the Mississippi River (Coon *et al.*, 1977), are less than the extreme age (> 100 yr) reported for *Margaritifera margaritifera* L. in Europe (Hendelberg, 1960), but are apparently similar to ages of other slow-growing species (Isley, 1914; Stansbery, 1971). Isley (1914) and Coker *et al.* (1921) reported that light-shelled species grow rapidly, and subsequent studies on *Anodonta* spp. and other thin-shelled species have confirmed their observations (Stansbery, 1961; Negus, 1966; Haukioja and Hakala, 1978). In comparison, they noted that growth in length of heavy-shelled species is most rapid in early life but slows considerably, such that growth lines become tightly spaced and difficult to differentiate. Coker *et al.* (1921) computed mean growth rates of roughly 6 mm/yr for medium-sized individuals of thick-shelled species (*Quadrula* spp.), and Isley (1914) observed shell growth to be roughly 1 mm/yr for older (larger), riverine individuals. Riverine populations of at least some mussel species therefore contain many older, slow-growing cohorts. Based on the slow growth, closely spaced annuli, and considerable longevity of mussels, it is imperative that specimens be accurately aged if exploitation potential or population statistics are to be assessed from age-class structure and abundance (Moyer, 1984).

Although the formation of growth bands is the key process that allows age determination, it is not well understood. Band patterns on freshwater mussel shells occur in two varieties, wide, dark bands at fairly regular intervals, and lighter bands that are irregularly spaced (Tevesz and Carter, 1980). The mechanism through which these bands are incorporated into the mussel shell is still unclear. Explanations for this mechanism have been put forth by several authors, and were reviewed by Lutz and Rhoads (1980), Tevesz and Carter (1980), and Day (1984). According to the hypothesis advanced by Lutz and Rhoades (1977) from research on marine molluscs, under conditions favorable to growth, bivalves add to their shells by the deposition of successive laminae of calcium carbonate and conchiolin, an organic-rich substance secreted by the mantle. Periods unfavorable for growth, such as winter in temperate regions, apparently produce changes associated with anaerobic metabolism that lead to the deposition of a thin, dark, organic-rich growth band in the valves. Conversely, the hypothesis presented by Coker *et al.* (1921) and summarized by Tevesz and Carter (1980) was developed through research on freshwater mussels. This hypothesis describes the "doubling-up" of shell layers resulting from mantle retraction and re-extension which produces the visible appearance of a dark ring on the shell. Hence, dark annual rings would be produced by the frequent "doubling-up" of the shell along growth edges produced by frequent growth interruptions from the onset or outset of cold weather (winter). Either of these hypotheses could explain the prominent annual rings that we observed, formed in winter and visible by late spring in Virginia.

There was no indication of long-term tagging or marking stress on shell growth of species recovered for age validation. Unmarked, freshly dead specimens and shells from muskrat middens showed growth increments and rates similar to those in tagged and marked shells of comparable ages (Moyer, 1984). Brousseau (1979) also reported no significant differences in growth rate between handled and unhandled softshell clams *(Mya arenaria* L.) Handling stress was reported in earlier studies with freshwater mussels (Isley, 1914; Coker *et al.*, 1921; Negus, 1966), and notching of bivalves can result in the formation of disturbance lines in shells (Lutz and Rhoads, 1980). Our handling and marking procedures probably resulted in some stress of mussels, and disturbance lines were formed on many specimens that we marked and later examined. These lines were less prominent than annuli and apparently were formed at the time of marking. However, there was no evidence, based on mussel behavior after marking in the laboratory and comparative growth between marked and unmarked specimens, that the stress was more than temporary.

Shell ashing and acetate peels, by the methods described, proved to be ineffective techniques for use on freshwater mussels. However, the combination of 5% HCl etching solution and 15-45 sec etching time provided some peels of suitable quality. Recent modifications and improvements in the acetate peel technique could now make this method more applicable to freshwater bivalves (Ropes, 1987), and further testing is warranted.

Thin-sectioning of shells was judged to be the most consistent and accurate technique for age determinations. Thin-sections provided the highest degree of resolution for all species examined, and for all sizes and ages, from 15 to 210 mm and 3 to 56 years. Annulus formation was readily apparent in cross-sections of marked shells, and true and false annuli could be easily separated. Minor shortcomings of the thin-sectioning technique were the 0.5 to 1 hr required to prepare a specimen for examination, the need for several cuts on large shells to fit the petrographic slides (27 x 46 mm) used in this study, and the difficulty in sectioning small shells (<20 mm). Because small, thin shells often were too brittle to withstand the pressure of the cutting blade or chuck used to hold the shell in place, we suggest that bioplastics be used for embedding the shells. Modification of the equipment or technique should overcome these minor problems.

We observed occasional inclusion of small particles of sediment in shells, which produced the formation of a thick, dark line internally and externally, especially on female *Villosa vanuxemi*, as noted previously. This band was a false annulus because it was incomplete and usually occurred only in the vicinity of the foreign particle. Its formation is perhaps evidence of the adventitious conchiolin layering reported by Beedham (1965) and reviewed by Tevesz and Carter (1980). Such layers are described as being a conchiolin-rich damage response mechanism, often found in unionids having thin-shelled umbonal areas. They apparently are produced to mitigate damage caused by extraneous water, sediment, or other material entering through an abnormal separation between the mantle and shell margin.

Our test of the growth ring method confirmed the inadequacy of this technique, as previously noted by Rhoads and Lutz (1980). Erosion and corrosion of shells, separation of true from false annuli, and difficulty in counting closely deposited growth bands in older shells produced consistent underestimates of specimen ages. These errors in age, even on shells with relatively clear annuli such as those of *Fusconaia cor* and *Pleurobema oviforme*, would undoubtedly occur with most other unionids and result in erroneous ages and, consequently, imprecise population statistics. Jones *et al.* (1978) cautioned that growth curves based on external growth lines probably underestimate growth rate in young clams and overestimate it in old ones. Our results with freshwater mussel shells support this conclusion and indicate that the growth ring method provides only an estimate of mussel ages at best, particularly for older cohorts. With the current availability of sectioning techniques to provide more accurate ages of unionids, we recommend that use of the growth ring method be discontinued for all but the younger age classes or rapidly growing species that are age-validated.

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INTRACAPSULAR DEVELOPMENT OF *THAIS HAEMASTOMA CANALICULATA* (GRAY) (PROSOBRANCHIA: MURICIDAE) UNDER LABORATORY CONDITIONS

RICHARD A. ROLLER[1] AND **WILLIAM B. STICKLE**
DEPARTMENT OF ZOOLOGY AND PHYSIOLOGY
LOUISIANA STATE UNIVERSITY
BATON ROUGE, LOUISIANA 70803, U. S. A.

ABSTRACT

Copulation and egg capsule deposition of *Thais haemastoma canaliculata* (Gray) and subsequent development of embryos to hatching were investigated. Adult *T. haemastoma canaliculata* deposited egg capsules, each containing approximately 3200 fertilized eggs. The number of capsules deposited by any one snail over several days varied between 20-30. The expected ontogeny of spiralean cleavage followed by gastrula, trochophore, and veliger larva occurred. The trochophore and veliger stages were easily distinguished from each other. No nurse eggs occur in this species. Hatching of planktotrophic veligers occurred within 13 days after capsule deposition at $25^0/_{00}$S and 25-26^{0}C. Capsule wall dry weight decreased significantly; whereas, capsule content dry weight increased during the intracapsular period, largely due to increased calcification of embryonic shells. Embryonic calcium levels increased 24 fold during the intracapsular period.

The Southern Oyster Drill *Thais haemastoma canaliculata* (Gray) (=*T. haysae*, Clench, 1927) (Abbott, 1974), is a muricid gastropod inhabiting estuaries along the Louisiana gulf coast. This species is the primary predator on the Eastern Oyster *Crassostrea virginica* (Gmelin), the only commercially important species of oyster in Louisiana. It is believed that *T. haemastoma canaliculata* represents the greatest hazard to the survival of *C. virginica* (Pollard, 1973), thus making the drill an economically important destructive agent to the oyster fisheries in Louisiana (St. Amant, 1938, 1957; Burkenroad, 1931). In recent years, salt water intrusions, caused by the dredging of the Mississippi River at the Gulf of Mexico, have allowed *T. haemastoma canaliculata* to migrate further into the oyster seed grounds thus reducing the economic feasibility of extensive oyster culture (Pollard, 1973; Van Sickle *et al.*, 1976; Smith, 1983). The predation of *T. haemastoma canaliculata* on oysters and the regenerative ability of its feeding mechanism in response to injury have been previously described (Garton and Stickle, 1980; Roller *et al.*, 1984). Seasonal changes in the reproductive component weights of the southern oyster drill indicate major episodes of capsule deposition occurring between April and August (Belisle and Stickle, 1978).

Considerable interest in the reproductive biology and embryology of prosobranch gastropods has stimulated research by various investigators for many years. These investigations have varied from complete descriptions of the embryological development of certain gastropods (Conklin, 1897; Pelseneer, 1911; D'Asaro, 1966) to descriptions of specific morphological and ecological relationships of various larval forms (Thorson, 1950; Mileikovsky, 1971; Fretter, 1972; Spight, 1977; Strathmann, 1980; Hadfield, 1984; Pechenik, 1984). St. St. Amant (1938) provided a well written account of the general biology of *Thais floridana haysae* (Clench) (= *T. haemastoma canaliculata*); however, very few figures were included in the work, and the thesis was never published. D'Asaro (1966), using light microscopy, gave an excellent discussion of the embryogenesis of *Thais haemastoma floridana* (Conrad). Belisle and Byrd (1980) used electron microscopy to investigate *in vitro* egg activation and development through hatching in *Thais haemastoma.* No investigation to date has attempted to combine the use of light and scanning electron microscopy (SEM) to view the copulation, ovipositioning, capsule structure, and developmental stages of *T. haemastoma canaliculata.* Furthermore, intracapsular weight changes prior to hatching have not been investigated. Knowledge of embryonic weight changes prior to hatching would yield valuable information concerning possible nutritive contributions of intracapsular components.

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[1] Present address: Department of Biology, University of Wisconsin, Stevens Point, Wisconsin 54481, U.S.A.

While considerable ambiguity exists concerning the exact taxonomic position and classification of *Thais* spp. of the Gulf of Mexico (Butler, 1985), the species examined in the present investigation was identified as *T. haemastoma canaliculata* (Gray) based on the presence of a large nodular shell possessing a strongly indented suture (Abbott, 1974). The objectives of the present investigation were to (1) observe copulation and capsule deposition of adult *Thais haemastoma canaliculata* in the laboratory; (2) determine the intracapsular developmental rate of embryos to hatching at a salinity (25$^0/_{00}$) and temperature (25^{0}C) similar to that experienced in the estuary; (3) examine changes in capsule structure and composition during development; and (4) rear hatched veligers.

MATERIALS AND METHODS

Adult *Thais haemastoma canaliculata* (shell length $>$ 40 mm) were collected monthly during 1982 and 1983 from Bay Champagne near Grand Isle, Louisiana, U.S.A. Snails were transported to the laboratory and placed into 38 *l* aquaria (30 snails/aquarium) containing artificial seawater (Instant Ocean® Sea Water Mix) at the temperature and salinity of the collection site (at time of collection). The seawater near Grand Isle fluctuates in salinity and temperature between 10 and 35$^0/_{00}$ and 10 and 30^{0}C, respectively, over the course of a year (Barrett, 1971); however, the aquaria were maintained at constant salinity and temperature during this investigation. The male:female ratio in each aquarium was approximately 1:1. The snails were maintained on a photoperiod similar to the natural conditions under which they were collected. Drills were fed oysters (*Crassostrea virginica*) and clams [*Rangia cuneata* (Sowerby)].

Copulation and capsule deposition in the aquaria were observed and photographically recorded. Capsules were removed from the aquaria as soon as possible. Since the capsules were covered by the foot of the snail during deposition it was often necessary to delay their removal from the aquaria for several hours.

Individual egg capsules of known age were transferred to separate, clean glass culture bowls (10 cm tall x 19 cm diameter) containing filtered (0.45 μm) seawater at the appropriate temperature and salinity. The seawater in each bowl was aerated and changed daily throughout the experiment. Five capsules were sampled daily for the determination of developmental rates. Iridectomy scissors were used to open the egg capsules. The embryos were removed with a pasteur pipet and placed on glass slides with clay-supported coverslips. Embryos were then examined and photographed with a Leitz Wetzlar Orthoplan compound microscope with an Orthomat camera attachment. Embryos obtained from individual capsules were examined to determine if development to hatching was synchronous within a particular capsule. Intact and opened capsules were photographed with a Wild TYP stereo-dissection microscope with a Nikon M35-S camera attachment. Intracapsular osmolarity was determined with a Wescor vapor pressure osmometer.

Two days after deposition, ten capsules were opened and the embryos were removed and counted. Approximately one day prior to hatching, 10 randomly selected capsules from each culture bowl were dissected for mortality determination.

Each culture bowl was examined daily for hatched veligers, which were then transferred to additional culture bowls containing freshly aerated and filtered sea water (1 larva/100 ml). The water in each bowl was replaced daily. Veligers were then fed 10^4 cells/ml (final concentration) daily of *Isochrysis galbana* (Parke) - *Monochrysis lutheri* (Droop) (1:1). Algae were cultured using the method of Guilliard (1975).

For scanning electron microscopy (SEM), embryos were removed from the capsules for fixation. Veligers were first anesthetized with $MgSO_4$ and then fixed for SEM. The best anesthetization was achieved by slowly adding small amounts (approximately 0.1g) of granular $MgSO_4$ to the culture water until the larvae were completely immobile but had not contracted or withdrawn into their shells. Specimens were fixed overnight with 2.5% gluteraldehyde in 0.2M sodium cacodylate-sucrose buffer (731 mOsm; pH = 8.0). The sucrose was used to adjust the osmolality of the fixative to the appropriate salinity of the culture in order to reduce osmotic stress during fixation. After fixation, the specimens were rinsed in three changes of distilled water to remove all buffer salts, dehydrated in acidified 2,2-dimethoxypropane (DMP), and transferred to modified Beem™ capsules with a 25 μm Nitex screen over each end. The specimens were then critical-point dried in CO_2, coated with approximately 200 Å of Au/Pd, and examined with a Hitachi S-500 scanning electron microscope at 25 KV. Empty egg capsules were sectioned with a razor blade and prepared as above for SEM investigation. For light microscopy, intact capsules containing embryos and larvae were fixed overnight in formalin-acetic acid-alcohol (FAA), dehydrated in ethanol, cleared with xylene, embedded in paraffin, sectioned at 7 μm, and stained with Azan (Humason, 1972).

For capsule dry weight analysis, random samples of 20 capsules were taken one day after deposition (Day 1) and three days prior to hatching (Day 10). The total length of each capsule was measured with a vernier caliper. Each capsule was briefly rinsed in distilled water and then dissected into two components: capsule wall and capsule contents (embryos and albumen). The components were then lyophylized and capsule wall dry weight, capsule content dry weight, and total capsule dry weight was determined to 0.001 mg using an analytical balance. Capsule component indices were then calculated by the method of Stickle (1973). The relationship between capsule length and dry weight was analyzed by simple linear regression (SAS Institute Inc., 1985a, b). Differences between Day 1 and Day 10 dry weight components were compared by a two-sample t-test (Steel and Torrie, 1980).

Embryonic calcium levels were analyzed by atomic absorption spectrophotometry (Perkin-Elmer Corp., 1982). Twenty capsules on Day 1 and Day 10 were dissected and the contents were incubated in 10 ml of a 1% LaO_3 / 5% HCl mixture (40^{0}C) for 1 hour to mobilize any calcium present. The contents of each capsule were then centrifuged. The supernatant was removed, diluted 2X with fresh LaO_3-HCl, and analyzed. Total inorganic material was determined on an additional sample of 20 capsules by ashing at 450^{0}C for 4 hours.

Total organic material was calculated by subtracting the total ash (inorganic) from the pre-combustion dry weight. Day 1 and Day 10 calcium, organic, and other inorganic levels were compared by a two-sample t-test (Steel and Torrie, 1980).

RESULTS

COPULATION AND CAPSULE DEPOSITION

Copulation in the drills was observed in the field from late April to late June, 1982 and from late April to early June, 1983. During these months snails were found in large breeding aggregations which extended from approximately 0.5 m above the water surface at low tide to 1 m in depths. The number of snails comprising each aggregation varied from 6 to 27 individuals. Drills collected in early June, 1983 began copulating in the laboratory within 5 days. The duration of copulation was variable, lasting from approximately 2.5 hours to 3 days. During copulation the male crawled onto the shell of its partner and inserted its penis into the right side of the mantle cavity. Spermatozoa and prostatic secretions were presumably discharged into the genital aperture of the female (Fretter and Graham, 1962).

Egg capsule deposition occurred as early as six hours and up to sixty days after copulation was observed. In the laboratory, the egg capsules were attached to the glass walls of the aquaria, usually near the exhalant port of the undergravel filter system. Rarely were capsules deposited on oyster shells; however, oysters covered with *Thais* egg capsules have been collected from Grand Isle. Capsule deposition was intermittent. Snails were observed to cease deposition for a while, feed on oysters, and then resume deposition, sometimes in an entirely different location. Snails tended to attach their capsules together forming one large communal mass. The intermittent feeding behavior as described above and the communal egg masses made distinguishing which female laid specific capsules difficult. The number of capsules obtained from any one snail varied; however, most drills deposited 20-30 capsules in a mass. The duration of capsule deposition also varied, from as short as 2-3 hours to as long as 6-7 days. Snails were also observed to pause during deposition and remain on the capsule mass without feeding for several hours before resuming capsule laying.

Capsules were usually attached by their bases (Fig. 1), and formed a single layer on the substratum. In several cases capsules were observed attached together at various locations along their lengths; however, attachment never obstructed the opercular opening of any capsule in a mass. Butler (1954) reported similar findings.

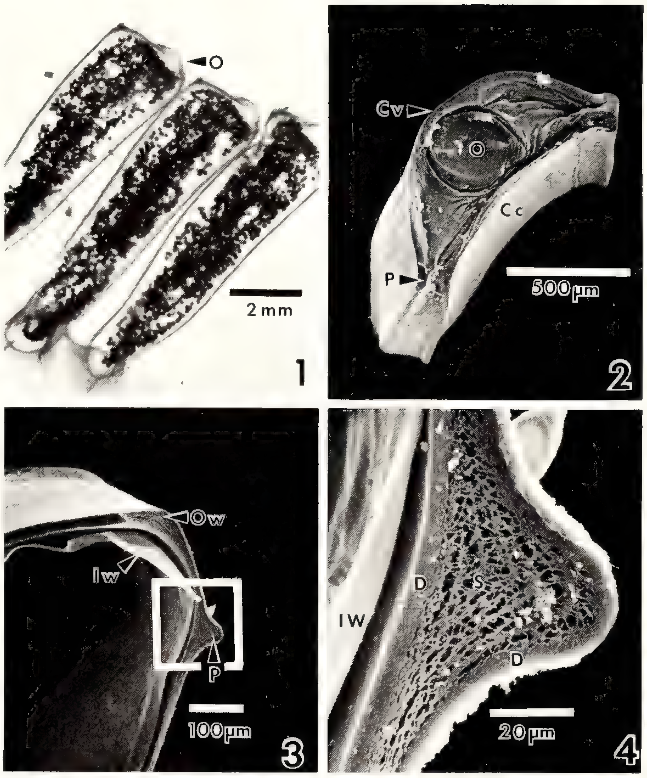


Fig. 1. Light micrograph of typical *Thais haemastoma* egg cases containing embryos. Hatching occurred approximately three days later (O, operculum). **Fig. 2.** Scanning electron micrograph (SEM) of an opercular view of an egg capsule (Cc, concave wall; Cv, convex wall; O, opercular plug; P, one lateral protuberance). **Fig. 3.** SEM of capsule cross-section showing both inner and outer walls (Iw, inner capsule wall; Ow, outer capsule wall; P, lateral protuberance). **Fig. 4.** SEM of capsule protuberance outlined in (3) (D, lateral dense layers of outer capsule wall; Iw, inner capsule wall; S, medial spongy mass of outer capsule wall).

The egg capsules of *Thais haemastoma canaliculata* are similar to those of *T. haemastoma floridana* as described by D'Asaro (1966). The capsules are somewhat conical in appearance, possessing a broad flat apical plate and tapering down to the base where they are typically attached to the substratum (Fig. 1). Each capsule possesses a convex and concave side along most of its length, giving the capsule an oblong appearance in cross section at the distal end (Fig. 2). However, the capsule is more circular in cross-section at its tapered base. Four longitudinal ridges (2 on each side) separate the convex and concave sides. The two ridges on each side merge at the apical plate forming a lateral protuberance (Figs. 2-4). Each capsule is composed of a thick fibrous-appearing outer wall and a thin membranous inner wall, which readily separate during microscopical preparation (Fig. 3). The entire outer capsule wall appears to be composed of two compact, dense lateral layers and a spongy-fibrous medial layer (Fig. 4). The protuberances and ridges represent sculpturing of the outer wall only and do not make up any portion of the inner wall, which encloses the embryos and the nutritive albumen. A round, discoidal opercular plug is located on the apical plate at the distal end of each capsule (Fig. 2). The operculum swells and bulges outward a few days prior to hatching. At hatching the operculum disintegrates leaving a prominent opercular scar.

Capsule length varied from 0.84-1.13 cm ($\bar{x}$ ± S.E. = 0.95 ± 0.01 cm; N=40). Capsule wall and capsule content dry weight varied from 0.47-1.57 mg ($\bar{x}$ ± S.E. = 1.05 ± 0.05 mg; N=40) and from 0.14-1.20 mg ($\bar{x}$ ± S.E. = 0.54 ± 0.04

mg; N=40) respectively. The total capsule dry weight varied from 0.92-2.14 mg ($\bar{x}$ ± S.E.= 1.60 ± 0.06 mg; N=40). Capsule wall and content dry weight comprised 65.6 ± 2.3 and 34.4 ± 2.3 ($\bar{x}$ ± S.E.) percent, respectively, of the total capsule dry weight. Capsule wall dry weight varied directly with capsule length: dry weight (mg)= −2.54 + (3.79 X length in cm) ($r^2=0.673$; N=40; $P<0.001$). A significant linear regression of total capsule dry weight on length also existed and is given as dry weight (mg)= −1.48 + (3.28 X length in cm) ($r^2=0.468$; N=40; $P<0.001$). No significant relationship existed between capsule content dry weight and capsule length ($P>0.05$). Each capsule contained 3246 ± 21 ($\bar{x}$ ± S.E.; N=10) embryos embedded in a viscous, albuminous fluid. Capsules, when deposited, were a milky white color, which during development turned light tan and finally dark brown just prior to hatching. Only three capsules deposited in the laboratory developed the dark purple color, characteristic of dead or stressed embryos (St. Amant, 1938; D'Asaro, 1966; Spight, 1977; Pechenik, 1982; Butler, 1954, 1985). Examination of these capsules revealed that all embryos were dead.

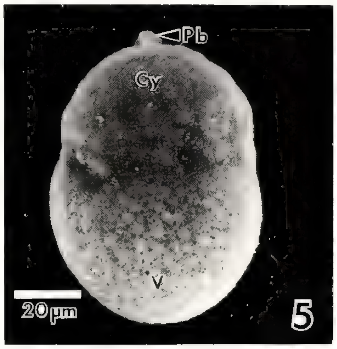
DEVELOPMENTAL RATE AND STAGES

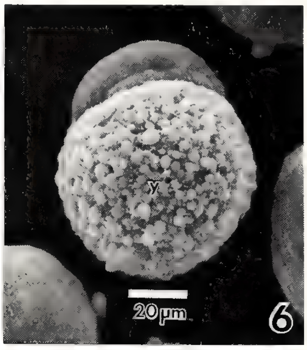
Development of *Thais haemastoma canaliculata* was synchronous within a particular capsule throughout the entire period of encapsulation and required 12-13 days to hatching at $25^0/_{00}$S and 25°C (Table 1). Unfertilized eggs were spherical and approximately 65-70 μm in diameter; however, as reported previously (St. Amant, 1938; D'Asaro, 1966), the majority of the yolk (deutoplasm) was concentrated in one pole (vegetal) with other cytoplasmic constituents being concentrated at the opposite (animal) pole. First and second polar body formation was complete within 2.5 hours after deposition of the capsule. By the second polar body stage (Fig. 5), the fertilized egg had elongated and the animal and vegetal areas were easily distinguished. The round yolk granules in the vegetal area were visible in live and preserved (Figs. 5, 6) zygotes. Early cleavage was restricted to the animal pole of the embryo. The first cleavage, producing the AB and CD blastomeres (Fig. 7) occurred 5-6 hours after deposition (Table 1). The second cleavage (Fig. 8) occurred within 2-4 hours after the first cleavage. As D'Asaro (1966) showed for *T. haemastoma floridana*, we found that the D blastomere possessed a large polar lobe (Fig. 8). Within 17-19 hours after capsule deposition, the 18 cell stage was complete. By that time, the polar lobe had been resorbed, and the large 2D macromere was seen (Fig. 9).

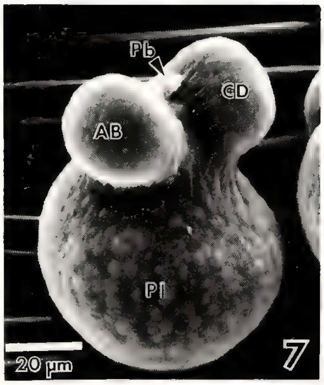
A stereoblastula containing a narrow segmentation cavity, as reported by St. Amant (1938), formed approximately 9-11 hours after polar lobe resorption (Table 1). Gastrulation by epiboly and archenteron formation (Fig. 10) was

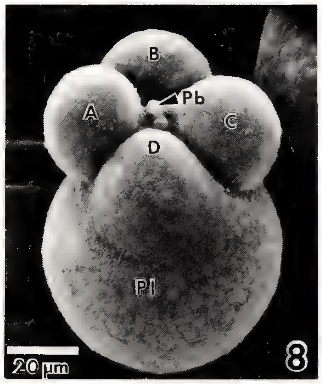
Table 1. Developmental rate of *Thais haemastoma canaliculata* at $25^0/_{00}$S and 25-26°C.

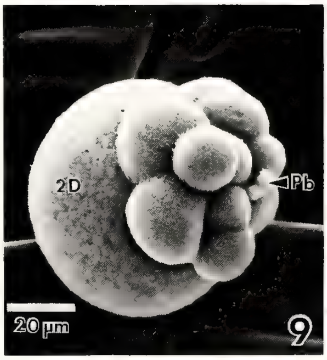
Developmental Event	Time
Fertilized egg with 2 polar bodies	2.5 hours
First cleavage	5-6 hours
Second cleavage	8-9 hours
16 cell stage	17-19 hours
Stereoblastula	28 hours
Early gastrula	3.5-4 days
Stomodael invagination, cephalic expansion & shell gland formation	5 days
Trochophore	5.5-6 days
Early veliger	7 days
Hatching	13 days











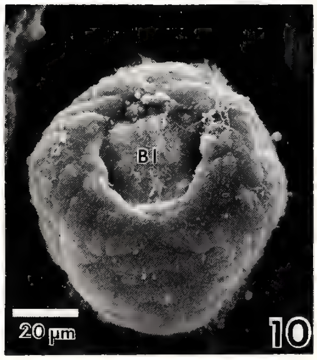


Fig. 5. SEM of fertilized egg after second polar body formation (Cy, cytoplasmic (animal) pole; Pb, polar bodies; V, vegetal yolk-containing pole). **Fig. 6.** SEM of vegetal view of ruptured polar lobe, illustrating dense yolk mass (y, yolk mass). **Fig. 7.** SEM showing first cleavage of the ovum, resulting in formation of AB and CD cells (Pb, polar bodies; Pl, polar lobe). **Fig. 8.** SEM of four-cell stage showing completion of A, B, C, and D cells with polar lobe (Pl) and polar bodies (Pb) still evident. **Fig. 9.** SEM of 2D cell, after polar lobe resorption (Pb, polar bodies). **Fig. 10.** SEM of gastrula stage, illustrating the blastopore (Bl).

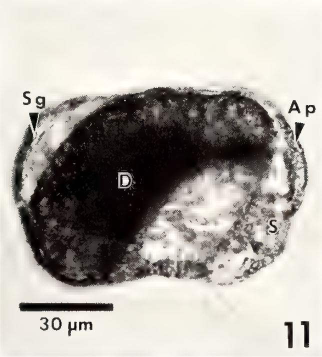
observed within 3.5-4 days after oviposition. Stomodaeal invagination, cephalic expansion, and formation of the shell field invagination (Fig. 11) occurred 5 days after deposition and followed the same pattern as described for *Thais haemastoma floridana* (D'Asaro, 1966).

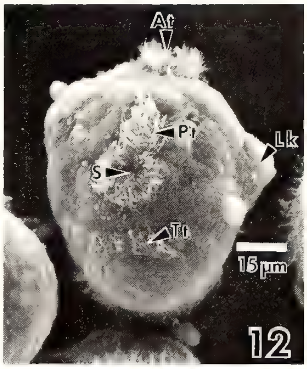
The early trochophore (Fig. 12) was characterized by a prominent stomodaeum, an apical tuft, the beginning of prototrochal and telotrochal ciliation, and the appearance of the larval kidneys. The late trochophore stage (Fig. 13) exhibited antero-posterior elongation, prominent larval kidneys, and well formed prototrochal, metatrochal, and telotrochal ciliation. The early veliger stage was characterized by the presence of the velar ciliation (Fig. 14). The dorsal margin of the shell gland was complete, and the protoconch covered the posterior region of the digestive gland's primordial cells. At this stage, the operculum was first evident (Fig. 15). By 8 days after capsule deposition, torsion, which results in a 180^0 rotation of the visceral mass, was complete. At this time, the apical ciliation and operculum were well developed, and the ventral foot and larval tentacles were first seen (Figs. 16-18).

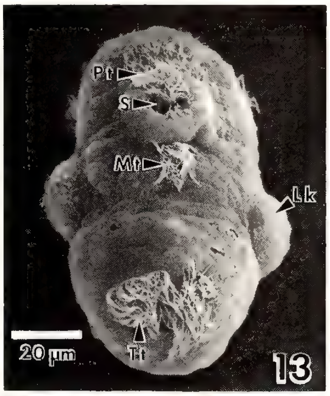
No nurse eggs, as described by Rivest (1983), were observed. The viscosity of the intracapsular contents declined over the course of the developmental period; however, the measured intracapsular osmolarity did not change during development. It is therefore possible that the intracapsular albumen is consumed by the embryos and replaced by sea water.

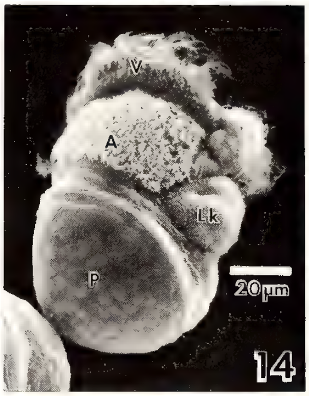
CAPSULAR CONTENT CHANGES DURING DEVELOPMENT

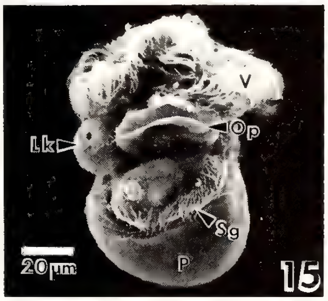
Capsule weight changes prior to hatching are illustrated in Table 2. During the intracapsular developmental period, the weight of the capsule contents significantly increased 63.0%; capsule wall weight decreased 43.4%; and the total capsule weight (contents and wall) decreased 18.4%. Total capsule ash significantly increased 37.8%, while total capsule calcium increased 24-fold over the encapsulated developmental period. Total capsule organic material significantly decreased 37.7%; however, other inorganic material (excluding calcium) showed a non-significant increase of 2.0%.











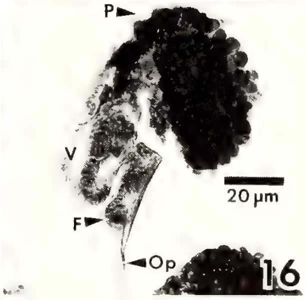


Fig. 11. Light micrograph showing stomodael invagination (S) and apical plate formation (Ap), immediately after gastrulation and prior to formation of trochophore (D, digestive system primordium; Sg, shell gland). **Fig. 12.** SEM of early trochophore stage (At, Apical tuft ciliation; Lk, larval kidney; Pt, prototrochal ciliation; S, stomodaeum; Tt, telotrochal ciliation). **Fig. 13.** SEM of late trochophore stage, showing formation of metatrochal ciliation (Lk, larval kidney; Mt, metatrochal ciliation; Pt, prototrochal ciliation; S, stomodaeum; Tt, telotrochal ciliation). **Fig. 14.** SEM of a dorsolateral view of early veliger larva (A, Apical ciliation; Lk, larval kidneys; P, protoconch; V, velum). **Fig. 15.** SEM illustrating a ventral view of an early veliger larva, illustrating shell operculum formation and prominent shell gland ciliation (Lk, larval kidneys; Op, shell operculum; P, protoconch; Sg, shell gland; V, velum). **Fig. 16.** Light micrograph illustrating a midsaggital section (7 μm) through a veliger (three days prior to hatching), showing further elongation of foot and operculum (F, foot; Op, shell operculum; P, protoconch; V, velum).

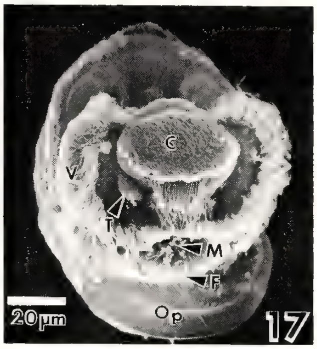
HATCHING AND REARING OF VELIGERS

Hatching of veligers (Figs. 17, 18) at $25^0/_{00}$S and 25^0C occurred between 12-13 days after capsule deposition. The shell length at hatching was 49.7 ± 8.3 μm. Hatching was accomplished through the dissolution of the capsule's operculum, possibly by mechanical means (St. Amant, 1938) or by chemical means (Sullivan and Bonar, 1984). Most (96-100%) embryos developed into normal appearing veligers and survived to hatching. In some capsules approximately 2-4% of the veligers were either dead or malformed at hatching. Hatched veliger larvae survived up to 50-53 days when kept in laboratory cultures and fed a mixture of *Isochrysis galbana* and *Monochrysis lutheri*. Ninety percent of the hatched veligers survived 45-50 days in culture. The shell length of the veligers after 37 days in culture was 122.4 ± 28.3 μm. No settlement/metamorphosis occurred, even though the larvae appeared healthy and fed on the algal species provided (Fig. 18).

Table 2. Capsule component weights on Day 1 and Day 10 for *Thais haemastoma canaliculata* capsules. Capsule components (in mg) are separated into organic, Ca^{2+}, and other inorganic components. N= 40 capsules.

	DAY 1	DAY 10	T VALUE
CAPSULE CONTENTS			
Organics	0.090 ± 0.005*	0.181 ± 0.004	14.84‡
Calcium	$5.60 \times 10^{-4} \pm 5.2 \times 10^{-6}$	0.161 ± 0.003	55.46‡
Other Inorganics	0.323 ± 0.012	0.332 ± 0.009	0.56 N.S.
Total	0.414 ± 0.044	0.675 ± 0.056	3.64‡
CAPSULE WALL			
Organics	1.218 ± 0.031	0.634 ± 0.039	11.69‡
Calcium	$6.41 \times 10^{-3} \pm 1.6 \times 10^{-4}$	$7.21 \times 10^{-3} \pm 1.0 \times 10^{-4}$	4.14‡
Other Inorganics	0.119 ± 0.004	0.119 ± 0.004	0.03 N.S.
Total	1.344 ± 0.033	0.760 ± 0.038	11.61‡
CAPSULE TOTAL (wall and contents)			
Organics	1.309 ± 0.056	0.815 ± 0.077	5.18‡
Calcium	$6.97 \times 10^{-3} \pm 8.9 \times 10^{-5}$	0.168 ± 0.003	54.46‡
Other Inorganics	0.443 ± 0.012	0.452 ± 0.010	0.56 N.S.
Total	1.759 ± 0.054	1.435 ± 0.001	3.29†

* - Mean ± S.E.
‡ - Statistically significant at α =0.001
† - Statistically significant at α =0.01
N.S. - Nonsignificant



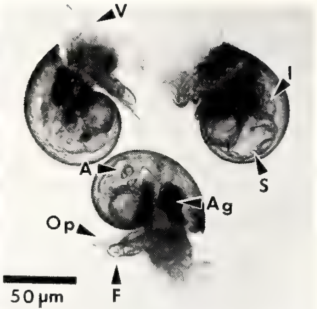


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Fig. 17. SEM showing an anterior view of a hatched veliger, illustrating a well developed velum (V), larval tentacle (T), and cephalic ciliation (C) (F, foot; M, mouth; Op, shell operculum). **Fig. 18.** Light micrograph of newly hatched veligers, illustrating prominent structures (A, algal cell in gut; Ag, anal gland; F, foot; I, intestine; Op, shell operculum; S, stomach; V, velar cilia).

DISCUSSION

We observed, with the aid of scanning electron microscopy, a distinct trochophore stage (Figs. 12, 13) for *Thais haemastoma canaliculata*. St. Amant (1938) had earlier reported that in *T. floridana haysae* the trochophore was atrochal and could not be distinguished from the early veliger stage; therefore, the early veliger could be identified only after the shell was formed. The development of the velum (Fretter and Graham, 1962), which is difficult to observe using standard light microscopy (St. Amant, 1938), is easily seen using SEM techniques (Figs. 12-15). The development of the protoconch is also more apparent from SEM observations (Fig. 14). St. Amant was unable to identify the onset of torsion in this species. We found that in *T. haemastoma canaliculata* torsion occurs prior to hatching, which agrees with D'Asaro's (1966) observations of *T. haemastoma floridana* development.

Belisle and Byrd (1980) identified two different cleavage patterns occurring in *Thais haemastoma*, as opposed to the one distinct pattern reported by St. Amant (1938) and D'Asaro (1966). In the present study, we failed to observe the second cleavage pattern observed by Belisle and Byrd (1980). The only cleavage pattern we observed agrees with that reported by D'Asaro (1966). The absence of the second cleavage pattern in our investigation does not deny its existence. This second pattern could be an infrequent deviation from the "normal" pattern usually observed.

The difference in developmental rate observed in the present study (13 days to hatching at $25^{0}/_{00}$S and 25-26°C) and that observed by Belisle and Byrd (1980) (16 days to hatching at $20^{0}/_{00}$ and 24°C) could be due to differences in experimental temperature and salinity. Belisle and Byrd (1980) did not specify the subspecies of snail they studied. The developmental patterns and rates we observed for *Thais haemastoma canaliculata* at $25^{0}/_{00}$S and 25-26°C are very similar to those reported for *T. haemastoma floridana* by D'Asaro (1966). The ranges of these two subspecies overlap and both are found on the Louisiana coast, although *T. haemastoma canaliculata* is more numerous (St. Amant, 1938). Butler (1954) made reciprocal crosses between the two subspecies and obtained normal larval development, suggesting that hybridization could occur in this area. Since the embryology of *T. haemastoma canaliculata* and *T. haemastoma floridana* is similar (St. Amant, 1938; Butler, 1954; D'Asaro, 1966; present study), the separation of the two into separate subspecies based on shell morphology alone is possibly unjustified. Further data, in the form of electrophoretic analysis, are needed.

Hatching of veligers, in the present study, occurred between 12-13 days after oviposition and was possibly accomplished by chemical dissolution of the capsule operculum, as occurs in the mud snail *Ilyanassa obsoleta* (Say) (Sullivan and Bonar, 1984). Veligers in laboratory culture survived 50-53 days after hatching but did not metamorphose. Algal cells were observed in the gut of the veligers (Fig. 18) and the larvae appeared healthy; however, none survived to settlement and metamorphosis. It is possible that the veligers did not obtain enough nutrients from the algal cells provided. The veligers did survive an extended time (50 days) and showed evidence of some growth (from 49.7 µm to 122.4 µm). Furthermore, the algal species and concentration provided have been sufficient for other planktotrophic larvae (Ament, 1979; Jespersen and Olsen, 1982; Sprung, 1984); however, the nutrient levels and quality necessary for maintenance could possibly not be sufficient for growth and metamorphosis. Hadfield (1984) showed that a high degree of substratum chemical specificity can be required to induce settlement and metamorphosis in molluscan larvae. Several chemical compounds, from naturally occurring substances, have been identified as inducers of larval settlement and metamorphosis (Morse *et al.*, 1979; Heslinga, 1981; Rumrill and Cameron, 1983; Morse and Morse, 1984). It is possible that one or more inducers exist for *Thais haemastoma canaliculata.* Such inducers could exist in encrusting algae on oyster shells or possibly in polychaete tubes or barnacles upon which young *Thais* prey. Oysters, tube-dwelling polychaetes, and barnacles are abundant along the Louisiana coast.

Gastropod species possessing teleplanic veligers could be dispersed over a large geographic range and would have a planktonic existance of long duration (Scheltema, 1978). It appears from our results and the observations of others (St. Amant, 1938; D'Asaro, 1966; Scheltema, 1978) that *Thais haemastoma canaliculata* veligers are teleplanic and are likely to survive as long in the field as they did in the laboratory.

The spongy/dense layering of the outer wall of the egg capsules could just be the result of the process used to form the capsule and have no specific function; however, in our opinion this layering appears similar to that seen in vertebrate long bones (Mader, 1985) and could possibly aid in lending strength and support to the capsules thus protecting the enclosed embryos against physical damage. The protuberances and ridges could aid in maintaining an upright capsule and further enhance the protection of the delicate embryos inside.

Egg capsule dry weight varied directly with capsule length ($r^2 = 0.673$; $P < 0.001$) for *Thais haemastoma canaliculata.* The dry weight of individual capsule components varied differently from ovipositioning to hatching. The overall decrease in total capsule dry weight during the intracapsular developmental period (Table 2), possibly reflects the loss of metabolic end products through the capsule wall. The weight of a single capsule operculum (unpublished data) is only 0.08 ± 0.02 mg (N = 20); therefore, the 43.4% decrease in capsule wall weight appears too high to be explained solely by chemical dissolution of the opercular cap. It is possible that portions of the inner matrix of the capsule wall are eroded prior to hatching; however, in this investigation all hatched veligers exited from the capsule through the operculum. It is therefore unlikely that erosion of other portions of the capsule wall would aid the hatching process by forming multiple exits. It is possible that nutrients or other substances are removed from the wall and utilized by the developing embryos. Since the majority of the capsule wall is composed of organic material (Table 2) and the uptake of dissolved organic material (DOM) by molluscan larvae has been documented (Manahan, 1983), this hypothesis is possible. This hypothesis could also aid in explaining the doubling of the capsule content organic weight; however, this is speculative since we have no confirming data. The dry weight of the capsule contents (albumen and embryos) significantly increased 63% prior to hatching. We have shown (Table 2) that much of this increase (24%) is due to the uptake of calcium by the embryos, presumably for calcification of the shell prior to hatching. Eyster (1986) showed that calcium was the main constituent of early shell mineralization for several species of gastropod veligers. Likewise, our data for *T. haemastoma canaliculata* support an observed overall increase in calcium content of these veligers prior to hatching. We found a small amount of calcium associated with the capsule wall (Table 2), which was probably due to residual calcium adsorbtion to the wall, or possibly a small number of embryos that we neglected to remove. None of the increase in capsular content dry weight (i.e. embryonic weight) was due to inorganic materials other than calcium. It is expected of marine organisms with planktotrophic larvae that most of the organic growth should occur after hatching and during the planktonic existence (Scheltema, 1967; Pilkington and Fretter, 1970; Pechenik and Fisher, 1979; Pechenik, 1980, 1984; Pechenik and Lima, 1984). We observed a significant doubling in the organic material of the capsule contents; however, we made no weight measurements of planktonic veligers. The increase in the organic material of the capsule contents could be related to the corresponding loss of organic material from the capsule walls; however we have no data to prove this assumption. It is clear that observations on growth and weight changes of planktonic stages is needed before any comparisons can be attempted.

It was the purpose of this study to add to earlier investigations of *Thais* developmental patterns, egg capsule structure, and weight changes over the course of intracapsular development. Our findings and those of St. Amant (1938), Butler (1954), D'Asaro (1966), and Belisle and Byrd (1980) illustrate the tremendous reproductive potential for this species. Even though the planktonic larval mortality must be quite high, when one considers the sheer number of embryos contained in a single capsule (about 3200), the number of capsules deposited by a single female (20-30), and the 96-100% survival to hatching (laboratory conditions), it is no surprise that this species is a serious economic threat to the oyster industry along the United States gulf coast.

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TEMPORAL AND SPATIAL VARIATION OF SHELL MICROSTRUCTURE OF *POLYMESODA CAROLINIANA* (BIVALVIA: HETERODONTA)

ANTONIETO TAN TIU[1]
DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF SOUTHERN MISSISSIPPI
SOUTHERN STATION, BOX 5018
HATTIESBURG, MISSISSIPPI 39406-5018, U. S. A.

ABSTRACT

Temporal and spatial variation of the microstructure of inner surface of shell, condition index and organic content of shell of the Carolina marsh clam *Polymesoda caroliniana* (Bosc) in three different Mississippi habitats are described and discussed in relation to one another and environmental conditions. Microstructure of the inner shell surface distal to the pallial line showed distinct seasonal variation but little spatial variation. Pseudospiral microstructure, on inner surface of shell undertucked by the periostracum, predominated over "normal" crossed-lamellar microstructures in cooler seasons. Presence and seasonal frequency of occurrence of complex crossed-lamella one inside the pallial line reflected habitat differences. It was consistently present in submerged clams, present only in June and September in wild clams, and absent in exposed clams. Survival and condition index of transplanted clams in submerged area were higher than those clams in areas often exposed to air. Condition index showed seasonal and spatial variation, while organic content did not.

The shell microstructure of a bivalve is determined by its genome. This genotype sets constraints that fix limits within which adaptive change can occur. Moreover, while basic molluscan shell microstructures are few (Taylor *et al.*, 1969, 1973; Gregoire, 1972; Carter, 1980; Watabe, 1981; Wilbur and Saleuddin, 1983; Carter and Clark, 1985), subtle variations within each structural category occur because details of shell crystallization can be influenced by environmental factors (Barker, 1964; Taylor *et al.*, 1969; Rhoads and Panella, 1970; Lutz and Rhoads, 1978, 1980; Carriker *et al.*, 1980; Carter, 1980; Prezant and Chalermwat, 1983; Lutz and Clark, 1984; Carter and Clark, 1985; Prezant and Tan Tiu, 1986; Tan Tiu, 1987; Tan Tiu and Prezant, 1987). Conservative shell microstructures can be important characters used to determine phylogeny (Carter, 1980). Furthermore, consistent, inducible microstructures could be used to monitor recent or past environmental conditions (Lutz and Rhoads, 1980). Thus, it is important to examine shell microstructural variations to reasonably evaluate the environmental significance of microstructural patterns. The goal of this study was to investigate the extent of shell microstructural variation, temporally and spatially, on the eurytopic Carolina marsh clam, *Polymesoda caroliniana* Bosc, 1801.

Aragonitic shells of Corbiculidae, like the marsh clam, consist of outer crossed-lamellar and inner complex crossed-lamellar layers, separated from each other by a distinct (or indistinct) myostracum (Taylor *et al.*, 1973). Shell microstructure of *Polymesoda caroliniana* has not been previously examined in detail except for the conchiolin layers within the shell (Kat, 1985). Taylor *et al.* (1973) briefly described the shell microstructure of a related species, *Polymesoda anomala* (Deshayes, 1855), from Ecuador.

MATERIALS AND METHODS

Specimens of *Polymesoda caroliniana*, ranging 11 to 43 mm maximum anterior posterior length, were collected seasonally (June, Sept, Dec 1985, Mar, June 1986) from a marsh at the Rod and Reel Fishing Camp, Old Fort Bayou, Jackson County, Mississippi, U.S.A. Each seasonal sample was treated similarly. Thirty specimens were shucked in the field. After shell length, height and width were measured, shells were preserved in absolute ethanol for later examination by scanning electron microscopy. Areas of inner shell surface examined and compared are shown in figure 1. Another fifty specimens were transported to the laboratory where

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[1] Current Address: Harbor Branch Oceanographic Institution, Inc., Division of Applied Biology, 5600 Old Dixie Highway, Fort Pierce, Florida 34946, U.S.A.

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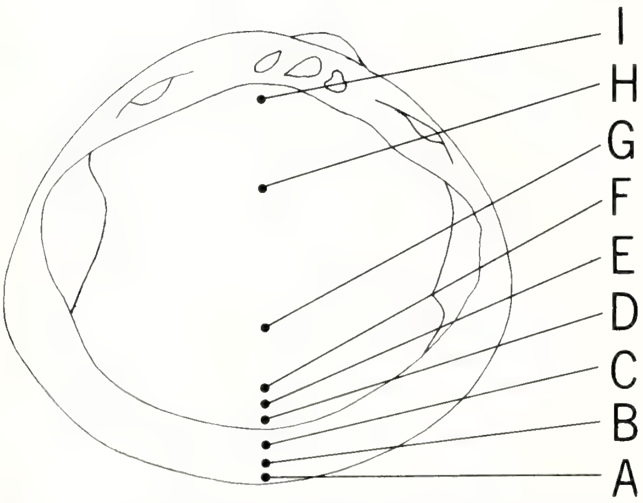


Fig. 1. Left valve of *Polymesoda caroliniana*. Areas of the shell surface examined are marked by dots, corresponding to the letters on the right (A, area undertucked by periostracum. B, area just dorsal to Area A. C, area between Area B and pallial line. D, E, F, the "transition zone". G, area at the level of ventral margin of adductor scars. H, area at the level of dorsal margin of adductor scars. I, area near umbo).

length, width, height, total weight with and without mantle water, shell and tissue dry weight, and organic content of shell were measured. Condition index and organic content of shell were computed. Definitions, procedures and care of specimens followed those by Prezant and Tan Tiu (1986) and Tan Tiu (1987).

A large sample of *Polymesoda caroliniana*, 11 - 43 mm long, collected in June 1985 from the Rod and Reel Fishing Camp, were marked and divided into two groups. One group was transplanted to a continually submerged area, and the other to a periodically exposed marsh area. Submerged and exposed areas are located within a 100 m radius of Halstead Bayou (adjacent to Gulf Coast Research Laboratory), Ocean Springs, Jackson County, Mississippi. Each group consisted of eight cages each containing 45 individuals. Details of procedures for marking, care of samples, size of cages and how they were set are similar to those described for studies of *Corbicula fluminea* Müller, 1774 by Tan Tiu (1987). Two cages were recovered from each site each season (beginning September 1985) at the same time wild samples were collected from the Rod and Reel Fishing Camp. Samples were treated as previously described. Because of high mortality, all cages in the exposed area were recovered in December 1985.

Monthly measurements of air, ground, surface and bottom water temperatures, water conductivity, dissolved oxygen, pH, methyl orange alkalinity, total filtrable residue, turbidity, transparency (Secchi depth), salinity, hardness, calcium, water depth and organic content of sediment were made in the three sampling areas. Water was absent in the emerged area on several occasions (June, July, Nov, and Dec 1985). Thus, water parameters could not be measured at those times. Details of methods used and errors of measurement are described in Tan Tiu (1987).

Significance of seasonal and habitat variation in condition indices and organic content of shell determined by one-way ANOVA, followed by Tukey test when ANOVA was significant. When only two samples were compared, t-test was used. Subjective evaluation was made in cases where statistical evaluation was not possible. All statistics were compared with critical values at $\alpha = 0.05$ and critical values used were conservative. Statistical methods used are described by Zar (1984).

Clams collected in the marsh at Rod and Reel Fishing Camp from June 1985 to June 1986 that were not in cages nor marked will be referred to as "wild" clams or group. Clams in cages transplanted to Halstead Bayou will be referred to as "experimental" groups. Experimental clams that were placed in the continually submerged area will be referred to as "submerged" clams or group, while clams that were placed in a regularly exposed area will be referred to as "exposed" clams or group.

RESULTS

ENVIRONMENT

The macroflora of the Rod and Reel Fishing Camp marsh (the location of seasonal wild samples and original source of experimental samples) and the exposed marsh area (a transplantation site), is predominantly *Juncus roemerianus* Scheele, while the submerged area (another transplantation site) was devoid of vegetation and had a muddy substratum. Turbidity, salinity, pH, calcium, total filtrable residue of water measured in the submerged area were significantly higher than at the Rod and Reel Fishing Camp (Table 1). During a few sampling periods (August to October 1985), when water was present in the exposed area, measurements of turbidity, conductivity, dissolved oxygen, methyl orange alkalinity and organic content of sediment were higher in the exposed area than in the submerged area at the same time. Temperature of water bottom, as measured by a maximum-minimum thermometer, ranged from 14.0 to 36.0°C in the submerged area and 7.9 to 42.2°C in the exposed area. Ground temperature measured at the bank of the submerged area ranged from 7.2 to 42.4°C. No maximum-minimum thermometer data are available in Rod and Reel Fishing Camp site.

SHELL MICROSTRUCTURE

Condescriptive statistics of the dimensions of shells examined by scanning electron microscopy are presented in Table 2. The inner shell surface of *Polymesoda caroliniana,* near the umbo (Area I), has irregular pits and grooves. Ventral to Area I (Areas G and H), the microstructures can be "clumped" into irregular mounds (Fig. 2), whose surficial borders represent areas where lamellae of opposing orientations meet (Fig. 3). The inner shell surface of areas G and H may be flattened with few mounds (Fig. 4), or underlain by irregular to granulate reticulated layers (Fig. 5).

The inner shell surface proximal to the pallial line (Areas D to I) can be divided into four microstructural types: complex crossed-lamella one, complex crossed-lamella two,

Table 1. Condescriptive statistics and t-tests of environmental variables measured at the Rod and Reel Fishing Camp and Submerged Area, Ocean Springs, Mississippi. Abbreviations in the variable column are as follows: surface water temperature (SWT), turbidity as measured by a nephelometer (Tur), water transparency as measured by a Secchi disc (Sd), conductivity (Con), dissolved oxygen (DO), salinity (Sal), methyl orange alkalinity (MOA), calcium (Ca), total filtrable residue (TFR), hardness (Hds) and sediment organic content (SOC). T-statistics of averages (with one standard deviation and n number of monthly measurements) are evaluated using critical values at α = 0.05 for (df) degrees of freedom. Min = minimum, max = maximum. Ho: Average values of environmental factors are the same in both places.

	Rod and Reel Fishing Camp					Submerged Area					Significance		
Variable	range min	range max	mean	standard deviation	n	range min	range max	mean	standard deviation	n	computed t	critical value	df
SWT (^{0}C)	19.5	40.0	25.9	6.1	13	9.0	31.0	23.4	6.9	13	Student's t = 0.976	2.064	24
Tur (NTU)	4.4	20.0	8.0	4.4	12	5.0	26.7	12.9	6.8	12	Student's t = 2.118	2.074	22
Sd (cm)	30	93	66	23	12	35	65	46	11	11	Welch t = 2.823	2.120	16
Con (μmhos/cm)	100	12000	4898	4282	13	750	24000	8142	8901	13	Welch t = 1.184	2.110	17
DO (mg/L)	0	10.0	5.9	2.4	13	4.0	8.9	6.9	1.3	13	Welch t = 1.228	2.093	19
Sal (o/oo)	0	9.0	2.2	3.5	13	0	18.0	9.5	5.3	13	Student's t = 4.127	2.064	24
pH	6.2	7.6	6.7	0.6	12	6.6	8.5	7.4	0.6	12	Student's t = 2.689	2.074	22
MOA (mg $CaCO_3$/L)	5.0	77.5	30.8	21.8	13	4.0	22000.0	1738.4	6087.9	13	Welch t = 1.011	2.179	12
Ca (mg $CaCO_3$/L)	6.2	246.0	88.9	80.8	10	23.7	613.3	301.6	236.6	10	Welch t = 2.690	2.201	11
TFR (mg/L)	100.0	8100.0	3553.9	2749.8	13	433.0	21866.0	12377.0	7820.2	13	Welch t = 2.838	2.145	14
Hds (mg $CaCO_3$/L)	31.0	8200.0	1736.0	2969.7	8	92	13433.3	3124.0	4236.0	8	Student's t = 0.759	2.145	14
SOC (%)	11.6	29.06	24.09	6.06	12	6.51	14.90	9.85	2.17	12	Welch t = 7.667	2.160	13

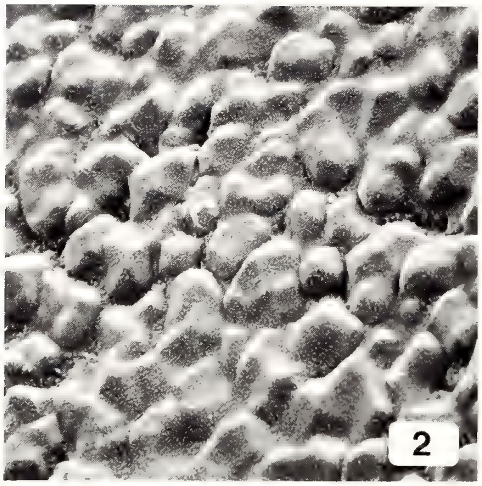
complex crossed-lamella three and reticulate microstructure. Microstructure of the inner shell layer (Fig. 5) is always of the reticulate type.

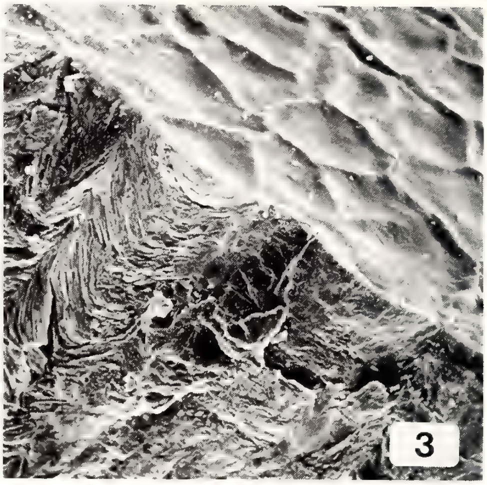
Exposed tips of secondary lamellae in complex crossed-lamella one are variably shaped with broad surfaces, and are oriented almost parallel to the shell surface (Fig. 6). Exposed tips of secondary lamellae in complex crossed-lamella two are narrow and also variably shaped, oriented irregularly or obliquely to the shell surface (Fig. 7). Exposed tips of secondary lamellae in complex crossed-lamella three are also irregularly shaped, oriented almost perpendicular to the shell surface (Fig. 8) with lamellae extending farther out to the inner surface of shell than the neighboring lamellae. Reticulate shell microstructure consists of loosely to densely packed thin or thick meshwork that can be granulated (Fig. 9).

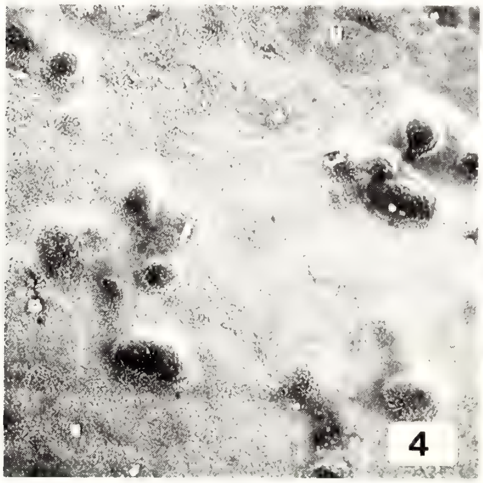
The microstructure of the inner shell surface in Area G can be grouped into irregular blocks (Figs. 10, 11). There is usually no detectable microstructure that represents a transition at the presumed "transition zone" (Areas D to F, just dorsal and adjacent to the pallial line) since this zone is frequently eroded. Thus, the dorsal boundary of the outer shell layer can be recognized as an elevated border or ridge along the curved antero-posterior axis. A convenient boundary between outer crossed-lamellar and inner complex crossed-

Table 2. Lengths of wild and caged *Polymesoda caroliniana* from Ocean Springs, Mississippi, whose internal shell surface microstructure was examined by scanning electron microscopy. Length measurements are in millimeter (min = minimum, max = maximum, S = submerged, E = emerged).

Date	Mean	Standard deviation	Range min	Range max	Total clams examined (n)
WILD					
June 1985	27.6	8.2	15.3	41.0	20
Sept 1985	29.3	4.9	20.0	37.6	29
Dec 1985	27.5	7.5	16.4	37.0	10
Mar 1986	33.4	4.5	24.5	38.5	10
June 1986	33.4	4.9	24.1	41.6	10
CAGED (S)					
Sept 1985	31.4	4.7	23.1	37.8	10
Dec 1985	34.1	3.3	27.3	41.5	30
Mar 1986	32.4	3.6	27.7	37.4	10
June 1986	34.7	5.2	29.2	41.5	10
CAGED (E)					
Sept 1985	30.8	3.7	25.2	36.0	10
Dec 1985	29.5	4.8	23.4	38.0	10







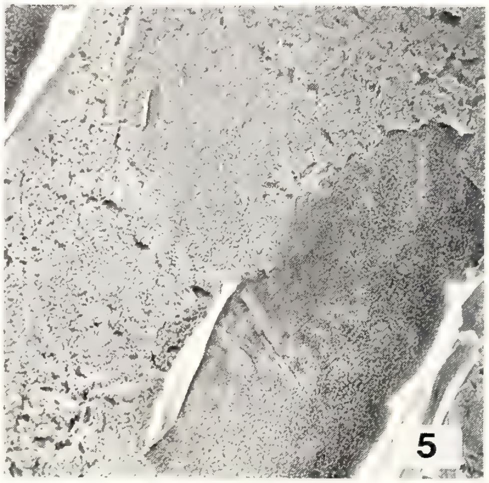


Fig. 2. Microstructures of inner surface of shell dorsal to the pallial line are grouped into irregular mounds. Mounds represent first order lamellae [Horizontal field width (HFW) = 352 μm. **Fig. 3.** Angular view of shell fracture dorsal to the pallial line. Second order lamellae of first order lamellae are oriented opposite to each other (HFW = 587 μm). **Fig. 4.** Few mounds are visible on rough surface of inner shell (HFW = 587 μm). **Fig. 5.** Irregular layers on surface of inner shell consists of reticulated microstructure (see Fig. 9) (HFW = 293 μm).

lamellar shell layers is therefore an eroded groove in place of an obvious pallial myostracum. This is evident at low magnifications (Fig. 12), where an apparent transition zone is seen only at a low magnification. Unlike the usually indistinct pallial myostracum, the adductor myostracum is distinct (Fig. 13). Both pallial (Fig. 14) and adductor (Fig. 15) myostraca can be traced sandwiched between the two shell layers.

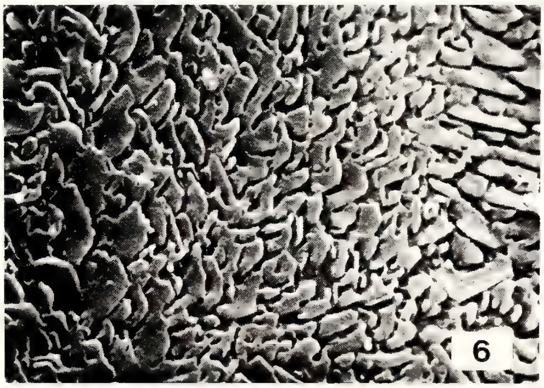
Ventral to the myostracum (Areas A, B and C), the microstructures of the inner shell surface of *Polymesoda caroliniana* and *Corbicula fluminea* (Prezant and Tan Tiu, 1985, 1986; Tan Tiu, 1987) are similar, except that no spiral shell formations were observed in *P. caroliniana* during colder seasons. Adjacent and ventral to the myostracum, Area C, the exposed lath tips are irregularly arranged. Area C is often covered by an organic matrix that render the underlying structures indistinct. Laths in Area B, dorsal and adjacent to the area undertucked by the periostracum, are arranged regularly to form second order lamella. Direction of the second order lamellae are opposite to that of the adjacent first order lamella. Microstructure of the inner shell surface of both Area B and C are referred to as crossed-lamella two (Table 3). Reticulate microstructure with loosely arranged strands can be observed at times on Area B. The predominant microstructure of the inner shell surface in Area A (undertucked by periostracum) is crossed-lamella one in all three groups. Exposed tips of secondary lamellae in crossed-lamella one are irregularly arranged, neither forming rosette nor pseudospiral pattern. Microstructure C, a collective term of convenience referring to pseudospiral (Fig. 16) and rosette microstructure in *Polymesoda caroliniana*, is similar to that of microstructure C in *Corbicula fluminea*, except that in the former, no complete spiral was observed. In *P. caroliniana*, two arc-shaped secondary lamellae (Fig. 16) can be joined to one another to form an approximate circular structure. When overlain by organic matrix, the identity of each arc can be obscured, thus appearing as a continuous circular flat band. The tertiary lamellae, composing the hub of the arc secondary lamellae are sometimes not aligned, such that the tertiary lamellar tips protrude at varying lengths into the central space of the circular structure. Therefore, the shape of the spaces enclosed by the secondary lamellae vary depending upon the degree of curvature of the secondary lamellae.

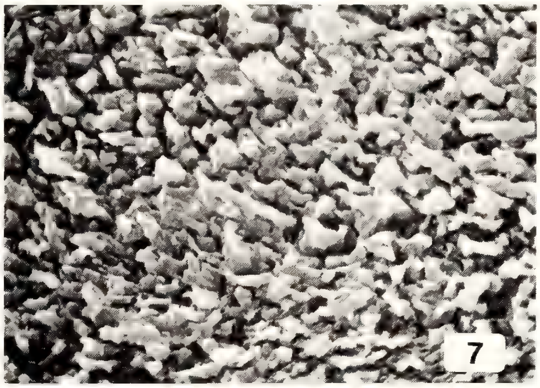
Seasonal and habitat variations in the microstructure of the inner shell surface of caged and uncaged *Polymesoda caroliniana* are summarized in Table 3. Over the 13 month period, microstructure C in wild clams was absent in June of 1985 and 1986, and its frequency of occurrence peaks in March 1986 (Table 3). The frequencies of occurrence of the following microstructures were highly correlated ($r >$ critical values at $r_{0.05(2)3} = 0.878$) in wild clams: microstructure C negatively correlated with crossed-lamella one and complex crossed-lamella one. Other microstructures of the inner shell surface did not show distinct seasonal patterns. Microstructure C was negatively correlated, whereas complex crossed-lamella one ($r = 0.941$) was positively correlated significantly with temperature of surface water at the time of sampling than the temperature average per season.

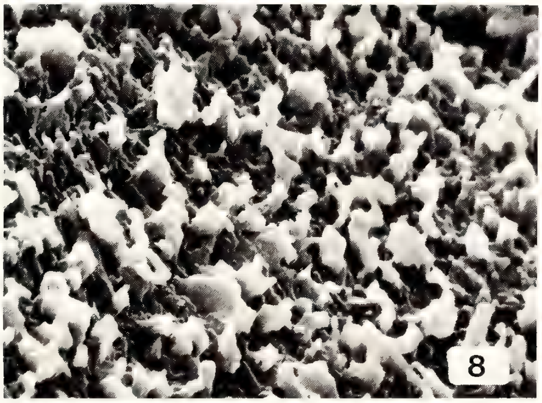
During the four seasons over the 12 month period, microstructure C in submerged clams was absent in September 1985 and June 1986, but its frequency of occurrence also peaks in March 1986 like that of wild clams (Table 3). Frequency of occurrence of crossed-lamella one was negatively correlated with that of microstructure C. Other microstructures of the inner shell surface did not show distinct

Table 3. Temporal and spatial variation of internal shell surface microstructure in *Polymesoda caroliniana*, Jackson County, Mississippi. Headings stand for areas of shell examined (first row) and shell microstructural type (second row). Shell microstructure abbreviations are: C, microstructure C; CL, crossed-lamella; CCL, complex crossed-lamella; Ret, reticulate. Frequency of occurrence expressed in percent, where 0 = 0%, 1 = 1 to 20%, 2 = 21 to 40%, 3 = 41 to 60%, 4 = 61 to 80%, 5 = 81 to 100%.

	Area A		Areas B-C		Areas G-I			
	C	CL1	CL2	Ret	CCL1	CCL2	CCL3	Ret
Rod and Reel Fishing Camp (wild)								
June 1985	0	5	5	0	1	0	5	0
Sept 1985	1	5	5	1	1	3	2	1
Dec 1985	2	3	5	0	0	3	3	1
Mar 1986	3	3	5	1	0	2	1	3
June 1986	0	5	5	0	1	1	1	3
Submerged Area (caged)								
Sept 1985	0	5	5	0	2	3	1	1
Dec 1985	1	4	5	1	1	2	2	2
Mar 1986	3	3	4	1	1	2	2	3
June 1986	0	5	5	0	1	1	1	4
Exposed Area (caged)								
Sept 1985	1	5	5	0	0	2	2	2
Dec 1985	3	3	4	1	0	3	0	3







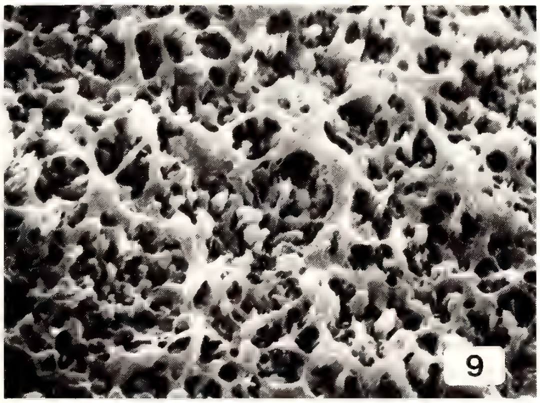
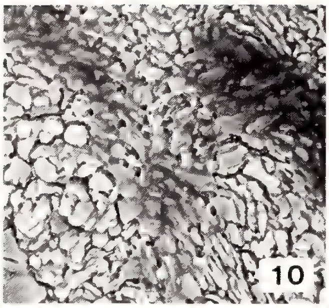
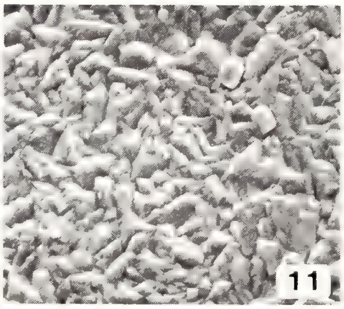
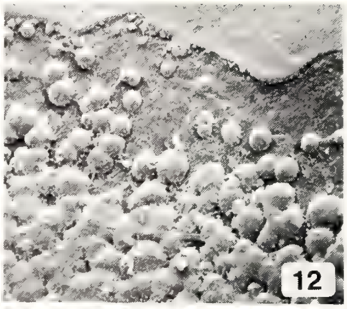
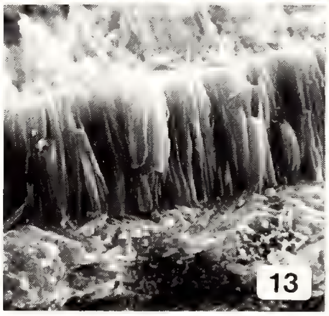


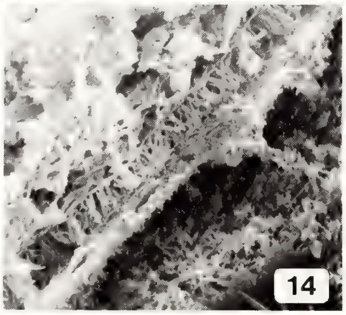
Fig. 6. Complex crossed-lamella one (HFW = 22 μm). **Fig. 7.** Complex crossed-lamella two (HFW = 22 μm). **Fig. 8.** Complex crossed-lamella three (HFW = 22 μm). **Fig. 9.** Reticulate microstructure (HFW = 22 μm).











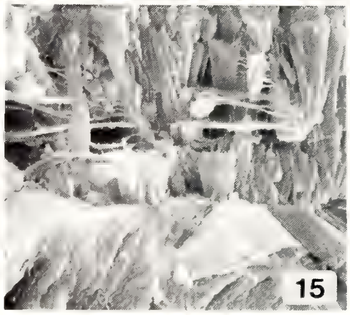


Fig. 10. Irregular blocks with smooth surfaces (HFW = 79 μm). **Fig. 11.** Irregular blocks with component secondary lamellae (HFW = 158 μm). **Fig. 12.** The groove is a convenient boundary between crossed-lamella (above) and complex crossed-lamella (below) (HFW = 790 μm). **Fig. 13.** Adductor myostracum consists of tall prisms. Remnant of adductor muscle at top of photo (HFW = 31 μm). **Fig. 14.** Organic compartments of pallial myostracum are sandwiched between naturally eroded shell layers (HFW = 16 μm). **Fig. 15.** Adductor myostracum is sandwiched between outer shell layer, crossed-lamella (above), and inner shell layer, complex crossed-lamella (below) (HFW = 32 μm).

seasonal pattern.

In exposed clams, available data on microstructure of the inner shell surface for September and December 1985 indicated that increase in the frequency of occurrence of microstructure C and decrease in crossed-lamella one were similar to those in wild clams. However, complex-crossed lamella one that was consistently present in submerged clams, present only in June and September in wild clams, were absent in exposed clams.

CONDITION INDEX AND ORGANIC CONTENT OF SHELL

Average percentages (± one standard deviation, n) of condition indices in wild (June 1985 = 3.30 ± 0.97, n = 44, Sept 1985 = 2.64 ± 0.95, n = 45, Dec 1985 = 2.87 ± 0.96, n = 49, Mar 1986 = 4.00 ± 1.17, n = 50, June 1986 = 4.38 ± 0.99, n = 50), and submerged bivalves (Sept 1985 = 3.64 ± 1.53, n = 37, Dec 1985 = 4.60 ± 1.11, n = 11, Mar 1986 = 6.22 ± 1.06, n = 4) varied significantly as tested by ANOVA (Tables 4). In exposed clams, samples were available only for September 1985 (5.14 ± 0.80, n = 6). The Tukey test indicates that the condition index in wild clams can be divided into three groups; June-1985, September 1985, and March 1986-June 1986. Tukey test could not determine how the December condition index was related to either June or September 1985 groups (at least one type II error has been committed) (Table 4). Condition indices in submerged clams can be divided into September 1985 and March 1986 groups. A Tukey test could not determine how the December condition index was related to either September or March groups (Table 4).

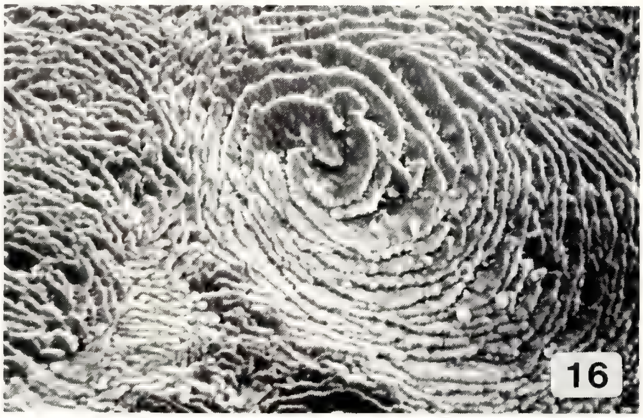


Fig. 16. Arc-shaped secondary lamellae can join to form a hub in Area A (area undertucked by the periostracum) during cooler months (Dec. and Mar.) (HFW = 16 μm).

The condition index in December 1985 was significantly different among wild, submerged and exposed clams. Moreover, the Tukey test indicated that the condition index in wild clams was different from submerged and exposed clams (Table 5). A pairwise comparison of average condition index in wild and submerged clams also indicated that condition index in September (Welch $t = 3.522 > t_{0.05(2)7} = 2.365$) and March (Student's $t = 3.661 > t_{0.05(2)52} = 2.007$) were significant.

Analysis of variance of average percentages (± one standard deviation, n) of organic content of shell did not show

Table 4. Temporal variation of means ($\bar{x}$) of condition index (CI) and shell organic content (SOC) in *Polymesoda caroliniana* from Rod and Reel Fishing Camp (wild) and submerged area (submerged), Ocean Springs, Jackson County, Mississippi.

						Analysis of Variance (one-way)						Tukey test
						Computed value			Table value			
	6/85	9/85	12/85	3/86	6/86	N	D	F	F	N	D	Overall conclusion
CI												
Wild	3.30	2.64	2.87	4.00	4.38	4	235	25.83*	2.85	4	200	$\bar{x}_1 \neq \bar{x}_2 \neq \bar{x}_4 = \bar{x}_5$
Submerged		3.64	4.60	6.22	—	2	49	6.95*	4.01	2	45	$\bar{x}_1 \neq \bar{x}_3$
SOC												
Wild	2.72	2.83	2.87	2.84	2.75	4	236	1.19	2.85	4	200	not necessary
Submerged		2.74	2.58	2.73	—	2	47	1.45	4.01	2	47	not necessary

*The ratio of the group mean square over the error mean square (F) with N and D degrees of freedom respectively is significant at $\alpha = 0.05$. When degrees of freedom fall between two table values, the lower value is used. CI and SOC are in %. Subscripts for $\bar{x}$ correspond to the order (left to right) of the means. Absence of available data is represented by blank spaces (before) and — (during) the sampling period.

Table 5. Tukey test among the average condition indices (CI) of *Polymesoda caroliniana* in three different habitats for December 1985. Computed studentized range (q) = ($\bar{X}_B - \bar{X}_A$) ÷ standard error. Critical value = 3.399 at $\alpha = 0.05$, degrees of freedom = 65 = 60, and total number of means tested = 3 (S = submerged, E = exposed area).

Habitat			Wild	Caged (S)	Caged (E)
Samples ranked by means (i)			3	2	1
Ranked sample means ($\bar{x}_i$)			2.87	4.60	5.14

Comparison (B vs A)	Difference ($\bar{X}_B - \bar{X}_A$)	Standard error	q	Conclusion
1 vs 3	2.27	0.26	8.73	Reject Ho: $\bar{x}_1 = \bar{x}_3$
1 vs 2	0.54	0.23	2.35	Accept Ho: $\bar{x}_1 = \bar{x}_2$
2 vs 3	1.73	0.32	5.41	Reject Ho: $\bar{x}_2 = \bar{x}_3$

Overall conclusion: $\bar{x}_1 = \bar{x}_2 \neq \bar{x}_3$

significant seasonal differences in wild (June 1985 = 2.72 ± 0.41, n = 48, Sept 1985 = 2.83 ± 0.38, n = 45, Dec 1985 = 2.87 ± 0.56, n = 49, Mar 1986 = 2.84 ± 0.40, n = 50, June 1986 = 2.75 ± 0.23, n = 49) (Table 4) and submerged clams (Sept 1985 = 2.74 ± 0.29, n = 35, Dec 1985 = 2.58 ± 0.16, n = 11, Mar 1986 = 2.73 ± 0.13, n = 4) (Table 4). In exposed clams, samples were available only for Sept 1985 (2.70 ± 0.19, n = 8). Average percentages of organic content of shell in Dec for wild, submerged and exposed clams were not significantly different as indicated by ANOVA ($F = 1.74 < F_{0.05(2)2,65} \approx F_{0.05(2)2,60} = 3.93$). Moreover, pairwise comparison of shell organic content in Sept (Student's $t = 1.167 < t_{0.05(2)78} = 1.991$) and Mar (Welch $t = 1.241 < t_{0.05(2)9} = 2.262$) between wild and submerged clams was not significant.

DISCUSSION

Among the microstructures of the inner shell surface in Table 3, complex-crossed lamella one reflects habitat differences. Complex-crossed lamella one was present throughout the year in submerged clams, present only during June and September in wild clams, and absent in exposed clams. Environmental conditions in these three habitats were different. The submerged area was less stressful than the exposed area. Of 360 individuals in each group (exposed and submerged), 45% were recovered alive from the submerged while only 13% were recovered from the exposed area. "Stress can be said to occur when physiological (or other) processes are altered in such a way as to render the individual less fit for survival" (Bayne, 1980). Moreover, shell formation is costly. Shell formation involves ion transport, protein synthesis and sequences of physiological processes (Wilbur and Saleuddin, 1983). "Healthier" clams would therefore be expected to have more energy allocated for shell formation and maintenance than less "healthy" clams.

Among the internal shell surface microstructures observed in this study, microstructure C and crossed-lamella one were the most conservative in the sense that seasonal patterns (frequency of occurrence) among the three groups wild, exposed and submerged clams were almost similar despite differences in habitat. Frequency of occurrence of microstructure C is inversely associated with temperature of water surface at time of sampling in wild clams, and with average temperature of water surface in submerged clams. Difference in time response could be due to temperature stability provided by water to submerged clams in a continually submerged habitat.

Other than what has been discussed above, the seasonal and habitat variation nor the factor associated with the presence and frequency of occurrence of microstructure in the inner shell surface is not clear. Reticulate microstructure did not show seasonal variation instead increased in all three types throughout the experimental period. This microstructure is possibly a common response to altered environment induced by several factors.

Palmer (1983) reported that production of skeletal organic matrix can be more "demanding metabolically than the crystalization of calcium carbonate." Therefore, high amount of organic content of shell is expected to occur during the time when clams are "healthiest". However, organic content of shell did not show significant seasonal variation. Possibly the difference if any during the study period were diluted by the total content through the life of the animal as suggested by an anonymous reviewer of this paper.

In view of the data presented here and elsewhere (Tan Tiu, 1987; Prezant and Tan Tiu, 1986), it seems that microstructure of the inner shell surface outside the pallial line, especially on Area A (area undertucked by periostracum), although showing seasonal variation and slight habitat variation, is characteristic of some species. That is, while *Corbicula fluminea* can form spiral shell microstructures, *Polymesoda caroliniana* cannot. Shell outside the pallial line could indeed be a conservative characteristic of the species, and therefore could be used in taxonomic or phylogenetic analyses. On the other hand, shell microstructure beyond basic components inside the pallial line, by virtue of its greater variability (changes in shell ultrastructure due to formation, modification, dissolution, etc.) as a reflection of changes in shell physiology due to environmental changes, can be used for taxonomic purposes only if ontogeny and environmental history are known. The variability of shell ultrastructure outside the pallial line in other corbiculids needs further study.

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THE USE OF ARM SUCKER NUMBER IN OCTOPODID SYSTEMATICS (CEPHALOPODA: OCTOPODA)

RONALD B. TOLL
DEPARTMENT OF BIOLOGY
THE UNIVERSITY OF THE SOUTH
SEWANEE, TENNESSEE 37375, U. S. A.

ABSTRACT

The average total number of suckers per arm for twelve species of octopodine cephalopods is presented in terms of the rate of sucker addition during growth. These data are shown to be useful for systematic analysis. The rate of sucker addition displays positive allometry relative to arm growth in early stages of development. Sucker addition slows to become negatively allometric in subadults and adults. New sucker morphogenesis ceases in the late stages of growth in some taxa resulting in an apparent species-specific sucker number. The hectocotylized arm displays a similar ontogenetic pattern of sucker addition.

Based on presumed reproductive isolation, general robustness, average arm sucker count (AASC), hectocotylized arm sucker count (HASC), and brooding mode, *Scaeurgus patagiatus* Berry, 1913 is removed from the synonomy of *S. unicirrhus* Orbigny, 1840 and is considered to be a separate species.

The total number of suckers on the arms of octopods is perhaps the second most salient meristic feature after the nominal character of the order (Octopoda = eight legs), which, being invariant among normal specimens, is of no systematic value among subordinal taxa. Counts of arm suckers occasionally were included as part of systematic descriptions and biological investigations of octopodid taxa, e.g. Férussac and Orbigny (1834-48), Troschel (1857), Verrill (1882), Jatta (1896), Naef (1923), Winckworth (1928), Sasaki (1929), and Boletzky (1975), but most contemporary workers have ignored this character. Furthermore, I am unaware of any published account that compares octopodids, either inter- or intraspecifically, based on sucker counts or that employs these data in broader comparative studies at any taxonomic level. The limited use of either total number of arm suckers or the number of sucker rows in systematic treatments of octopod taxa is difficult to comprehend. The situation can at best be rationalized by appreciating the time required to count the suckers on each arm of the numerous specimens required to construct a significant data base. The total number of suckers per individual can range from several hundred to several thousand depending on species and maturity.

Most recently, Roper and Voss (1983), in their precedent setting guidelines for the description of cephalopod taxa, included arm sucker count (ASC) as a minimal requirement for the adequate taxonomic description of octopodids. However, not one of the three papers cited by these authors as exemplary in octopod systematics include ASC data.

The arm sucker count of hatchling octopuses has been used as a specific-level systematic character (see Boletzky, 1977, 1984; Hochberg *et al.*, in press). The potential systematic value of arm sucker count in post-hatchling to adult octopodids remains inadequately investigated, an attribute shared by a large suite of other meristic and morphometric characters (e.g. gill lamellae number, penis morphology, alimentary tract anatomy, stellate ganglion morphology, etc.). The evaluation of ontogenetic rates of sucker morphogenesis also has been largely ignored, except for the most basic premises that larval octopods, whether benthic or planktonic, hatch with relatively few suckers compared to adults and that this sucker number increases with growth.

This paper presents a preliminary systematic survey of arm sucker counts in octopodine cephalopods. These results strongly suggest that average arm sucker counts can be valuable in systematic studies of the Octopodinae. The results also indicate that the rate of addition of new suckers shows a decidedly positive allometry with respect to arm growth in small animals. As a result, octopodids of relatively small body size precociously attain the majority of the adult complement of suckers. This phase is followed in late juveniles or early adults by negative allometry with a near to total cessation of addition of new suckers during the later stages of arm growth.

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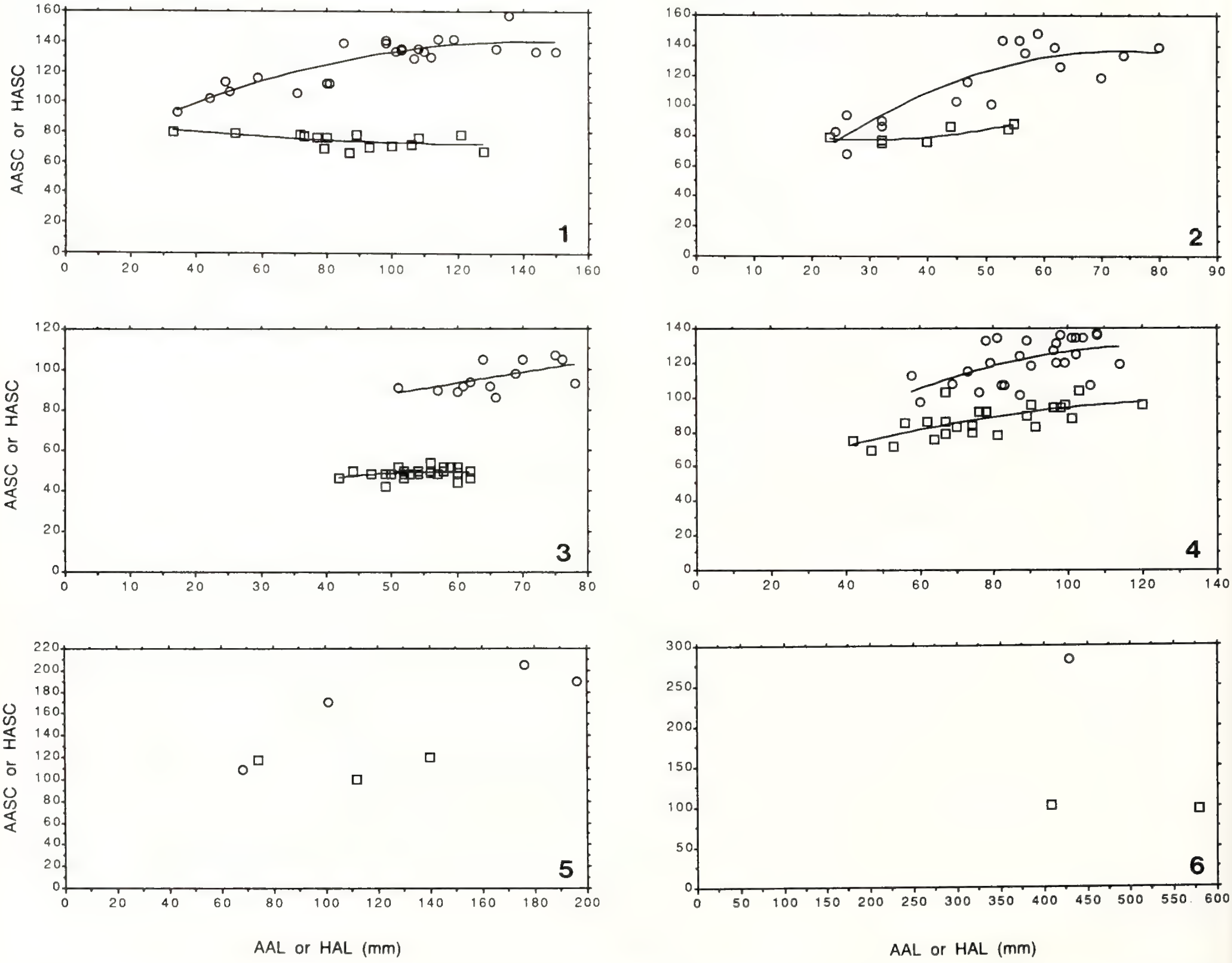
MATERIALS AND METHODS

The procedure used to count suckers was as follows. Suckers on each arm were counted starting at the mouth and moving to the tips. The relatively large suckers on the proximal two-thirds to three-quarters of the arm were counted using the unaided eye or an illuminated magnifier and passing a needle probe down the arm. Distally, where the suckers can be minute and densely packed, suckers were counted using a binocular microscope. A fine dissecting or insect pin was inserted into the arm as a marker during the transition between the two counting procedures. In all cases, sucker rudiments (anlagen), which appear as minute dome-like projections at the distal extremities of the arms, were counted as complete suckers. Suckers that were obviously missing, lost in combat with predators or prey or during capture, were counted as if present. Only complete arms with the entire distal tip intact were used to obtain sucker counts. Complete arms were considered 'available' and this term is used below. Arms regenerating from injury were excluded from consideration. To expedite counting, the number of sucker rows were counted and this value doubled to obtain the total sucker count for each individual arm. In cases of irregular sucker placement, a common artifact of preservation, this procedure could not be employed and it was necessary to count each sucker individually.

Arm lengths were measured using traditional methods with mechanical dividers and standard millimeter rules, following the guidelines re-established by Roper and Voss (1983). Average arm length (AAL) is the mean length of all available arms, with the exception of the hectocotylus. Average arm sucker count (AASC) is the mean of the number of suckers of all available arms with the exception of the hectocotylus. Both values are expressed to the nearest integer. Values



Figs. 1-6. Scattergrams of AASC vs. AAL and HASC vs. HAL for six species of Octopodinae [○ = unmodified (nonhectocotylized) arms; □ = hectocotylized arm; each symbol represents a single animal]. **Fig. 1.** *Octopus burryi.* **Fig. 2.** *Octopus hummelincki.* **Fig. 3.** *Octopus selene.* **Fig. 4.** *Octopus digueti.* **Fig. 5.** *Octopus defilippi.* **Fig. 6.** *Octopus dofleini.*

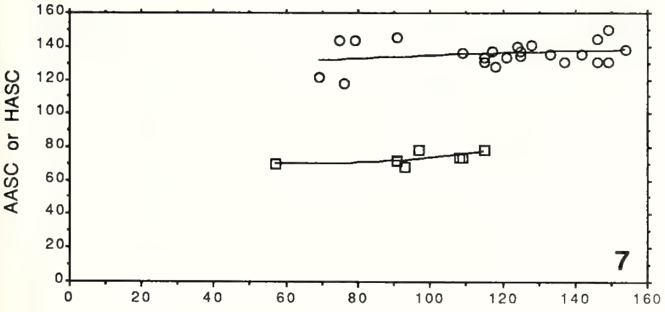
reported here are from individual animals with at least two available arms. Hectocotylus arm length (HAL) and hectocotylized arm sucker count (HASC) were separately recorded. All specimens examined were preserved in alcohol and most, if not all, were previously fixed in formaldehyde. Shrinkage of the arms is assumed to have occurred as a result of this chemical treatment (see Andriguetto and Haimovici, 1988). Scattergrams and statistical regression analyses were performed using a MacIntosh Plus© micro-computer with the statistical program Statworks 512+©.

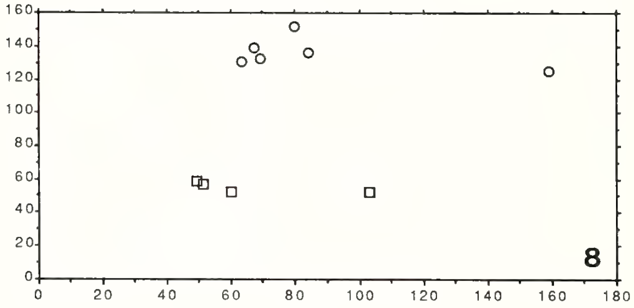
RESULTS AND DISCUSSION

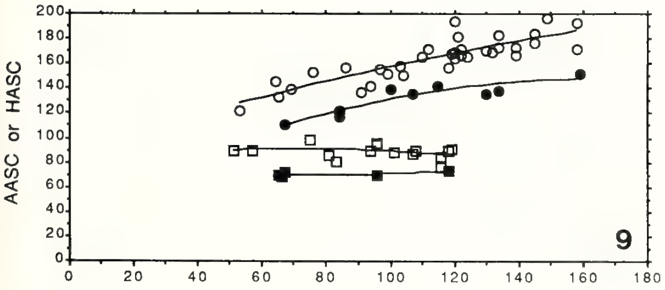
AAL, AASC, HAL, and HASC data from twelve species of octopodines are plotted in figures 1-11: *Octopus burryi* Voss; *O. hummelincki* Adam (=*O. filosus* Howell); *O. selene* Voss; *O. digueti* Perrier and Rochebrune; *O. defilippi* Verany; *O. dofleini* (Wülker); *Pteroctopus tetracirrhus* (delle Chiaje); *Robsonella fontanianus* (Orbigny); *Scaeurgus unicirrhus* Orbigny; *S. patagiatus* Berry; *Hapalochlaena* cf. *maculosa* (Hoyle); *Cistopus indicus* (Orbigny). Second-order regression lines are included for all data sets where n ≥5 (except *R. fontanianus*).

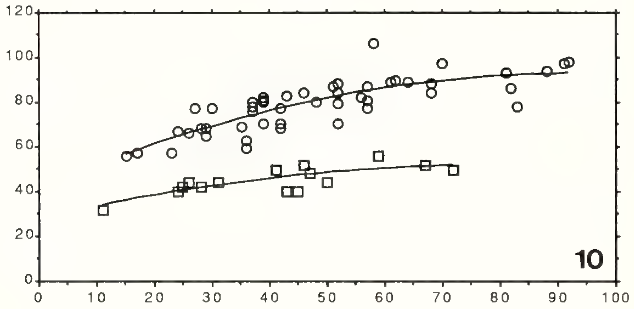
Preliminary regression analyses used each available arm on all animals as a separate datum, with the exception of the hectocotylus. The resultant scattergrams, combined with a basic understanding of octopod growth, showed that, for any one animal, arm sucker counts and arm lengths are autocorrelated, thereby jeopardizing the statistical validity of the regression. Individual averaging of the two data sets from each animal greatly reduced the size of the resulting data sets but served to enhance their robustness.

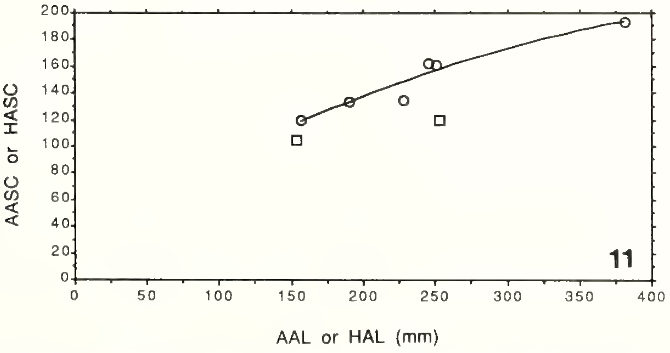
Larval and small juvenile specimens are absent from the present analyses, a reflection of the relative lack of representation of small individuals in museum collections and











Figs. 7-11. Scattergrams of AASC vs. AAL and HASC vs. HAL for six species of Octopodinae [○ = unmodified (nonhectocotylized) arms; □ = hectocotylized arm; each symbol represents a single animal]. **Fig. 7.** *Pteroctopus tetracirrhus.* **Fig. 8.** *Robsonella fontanianus.* **Fig. 9.** *Scaeurgus unicirrhus* (darkened symbols), *Scaeurgus patagiatus* (open symbols). **Fig. 10.** *Hapalochlaena* cf. *maculosa.* **Fig. 11.** *Cistopus indicus.*

the difficulty of identification of young octopodines. Therefore, the size ranges of some taxa included here are restricted to sub-adults and adults. Nonetheless, compared to the rate of arm growth (as a linear measurement), addition of arm suckers shows a distinct positive allometry during early growth stages. Small, presumably young, individuals have a disproportionately large percentage of their full adult complement of suckers. In *Octopus burryi* (Fig. 1), animals from 44-59 mm AAL had attained an average of 80.6% of the mean sucker count of animals from 98-119 mm AAL. Similar trends are seen in *O. hummelincki* (Fig. 2), *O. digueti* (Fig. 4), *O. defilippi* (Fig. 5), *Scaeurgus patagiatus, S. unicirrhus* (Fig. 9), *Hapalochlaena* cf. *maculosa* (Fig. 10) and *Cistopus indicus* (Fig. 11). AASC in *Octopus selene* (Fig. 3), *Pteroctopus tetracirrhus* (Fig. 7), and *Robsonella fontanianus* (Fig. 8) was statistically invariant over the size ranges reported here ($F = 2.29$, 0.71, and 1.81, respectively; $p > .05$). Most of arm suckers in small individuals are rudimentary or minute and densely packed along the arm tip. Arm growth proceeds by elongation and expansion at the tips, while the anlagen located there enlarge and become more widely spaced. Data from larger specimens show a negative allometric relationship between sucker addition and arm growth. Indeed, in the final stages of arm growth, very few if any new sucker anlagen are added and the number of sucker rudiments and minute suckers is reduced as the suckers enlarge to reach their definitive sizes.

Average sucker number appears to reach a maximum value in each species in an apparent display of determinant growth. These maxima differ among the species examined; however, while they are presumed to be genetically determined, it seems unlikely that future study will elucidate non-overlapping species-specific values because of the large number of octopodine taxa. Average sucker number data can, however, assist in identification and taxonomic delineation of taxa from restricted geographical areas or that are otherwise morphologically similar (see below). Furthermore, the reduction of the number and density of rudimentary suckers along the distal tip of the arms could be valuable in recognizing environmentally induced precocious onset of sexual maturation in undersized individuals, a matter of considerable importance in studies of the structure of wild populations as well as artificially induced maturation of laboratory cultured animals. The change from positive to negative allometry could coincide with important ecological or developmental changes yet to be recognized.

It is well known that among octopodid taxa the characteristic length of the arms varies with respect to body size (mantle length). Data presented here suggest that AASC and HASC also vary with respect to arm length among different taxa, apparently a function of both sucker size and linear density (compare Figs. 5, 6, 8).

The hectocotylized arm of males presents a special case. Without exception HASC was lower than AASC for all individuals of all taxa examined. The rudimentary calamus and ligula form early in ontogenetic development from the distal tip of the arm which is partially devoid of sucker anlagen. By the onset of calamus and ligula morphogenesis, sucker morphogenesis has slowed considerably and soon ceases. Therefore, the total sucker complement of the hectocotylized arm is less than, and is reached earlier in ontogeny than, any of the nonhectocotylized arms. Also, the most distal suckers are larger than those of the nonhectocotylized arms. HASC could, therefore, be a better taxonomic character despite its restriction to male individuals.

Each species appears to be characterized by a narrow range of values for HASC but, as with AASC, the large number of octopodid species probably precludes unique species-specific values. As with AASC, HASC also could be significant in restricted taxonomic applications (see below).

Reduction in length of the hectocotylized arm in comparison to the fellow arm of some taxa is well documented among the octopods. Also, the length of the modified portion of the arm varies among species, ranging from about 1 to 25% of the arm length. It is expected therefore, that the HASC varies among taxa independently of either general body size or lengths of the nonhectocotylized arms.

Analysis of AASC and HASC from a large collection of *Scaeurgus* spp. ($n=44$) (Fig. 9) provided unexpected and taxonomically provocative results. The Atlantic Ocean (Florida, Caribbean, Mediterranean) and Pacific Ocean (Hawaii, Japan) populations show distinctly different and non-overlapping values of AASC for same-sized individuals and of HASC for all-sized individuals. *Scaeurgus unicirrhus* was originally described by d'Orbigny (1840) from the Mediterranean Sea. Berry (1913) erected *Scaeurgus patagiatus* from the Hawaiian Islands, supplementing his description the following year (Berry, 1914). Berry recognized the slightly larger size of the Hawaiian form and the zoogeographic (reproductive) separation of the two populations. He felt this was sufficient grounds to separate them at the species level. Robson (1929) synonomized *S. patagiatus* with *S. unicirrhus*, remarking that all differences between the two were insignificant except for the greater arm lengths in the Pacific form. Subsequently *S. unicirrhus* has been reported from the Indian Ocean (Robson, 1929) and the Western Atlantic Ocean (Voss, 1951). It has not been reported from the eastern Pacific Ocean. The genus is restricted to tropical and warm temperate waters.

The Atlantic and Pacific forms of *Scaeurgus* are and probably have been reproductively isolated for an extended period of time, at least since the last closure of the Isthmus of Panama. The two populations differ substantially in maximum size, arm robustness, AASC, and HASC. Furthermore, the Pacific form is reported to brood its eggs by holding them within the web (W. Van Heukelem, pers. comm.; also see Boletzky, 1984), apparently an ususual behavior among octopodines (see Wells, 1978; Mangold, 1987). The more common practice of cementing the eggs to the substratum is displayed by the Atlantic form (Boletzky, 1984). I believe that the Pacific form merits the specific delineation recognized by Berry and correctly should be called *Scaeurgus patagiatus* Berry, 1913.

The relative simplicity of counting arm suckers facilitates routine examination even by inexperienced workers. Replicate sucker counts performed by novice assistants in the present study were routinely close, typically with errors of 2% or less. The greatest source of potential error involves the sucker rudiments on the arm tips. Some experience helps to standardize the counting procedure to include all true rudiments while excluding artifactual convolutions of the oral surface of the arm caused by fixation and/or preservation.

The use of total number of arm suckers rather than the number of sucker rows could be seen as arbitary in view of the biserial sucker arrangement found in all octopodines. Indeed, in many cases sucker rows were counted and multiplied by two to obtain total sucker number. However, the uniformity of the biserial arrangement often is lost in portions of some arms in many individuals. Also, in larval specimens and in adults of some taxa, the first several adoral suckers are uniserial (Howell, 1868; Naef, 1923). Finally, the use of total counts will facilitate future comparisons with octopodids with uniserial sucker arrangements (e.g. Eledoninae), and does not suggest an unwarranted homology between a single row of suckers of the biserial octopodines and individual suckers of the eledonids and related groups.

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RESEARCH NOTE

EFFECTS OF FIXATION AND PRESERVATION METHODS ON THE MORPHOLOGY OF A LOLIGINID SQUID (CEPHALOPODA: MYOPSIDA)

JOSÉ MILTON ANDRIGUETTO JR.
ZOOLOGY DEPARTMENT, UNIVERSIDADE FEDERAL DO PARANÁ,
CX.P. 3034, CEP 80.001, CURITIBA, PR., BRAZIL
AND
MANUEL HAIMOVICI
OCEANOGRAPHY DEPARTMENT, FUNDACÃO UNIVERSIDADE DO
RIO GRANDE, CX.P. 474, CEP 96.200, RIO GRANDE, RS., BRAZIL

ABSTRACT

The effects of freezing, fixation and preservation in 70% ethanol or 10% formalin for periods up to 46 months on body morphometry of *Loligo sanpaulensis* Brakoniecki, 1984, were investigated. Significant morphometric changes were observed, mainly between previously frozen and non-frozen specimens. Some forms of long-term preservation produced further, statistically significant changes. Long-term preservation increased variability of individual effects, widening confidence limits of most indices. Fresh squids or material recently fixed in a standard way should be used for population studies if there is no previous knowledge of the effects of fixation techniques on specific measurements.

Body proportions frequently are used as criteria for distinguishing groups of organisms in terms of species or populations. Morphometric indices are calculated from soft part measurements that are more subject to changes due to fixation and preservation in cephalopods, than, for example, in crustaceans and vertebrates. Therefore, care must be taken to recognize real differences as distinct from those caused by processing techniques.

In loliginids with worldwide distributions and closely related species and subspecies, morphometric indices have been used to identify and classify groups in taxonomic studies (Cohen, 1976; Voss, 1977; Juanicó, 1979) as well as to distinguish stocks or subpopulations (Kashiwada and Recksiek, 1978; Juanicó, 1979). Some papers, notably Cohen (1976), compared short-term effects on squid morphometric indices of refrigeration, fixation in 10% formalin, and preservation in isopropyl alcohol. Our paper deals with short and long-term changes on loliginid squids fixed and preserved in 10% formalin and 70% ethanol, with and without previous freezing.

MATERIALS AND METHODS

The effects of fixation and preservation on measurements and consequently on morphometric indices were analysed on samples of *Loligo sanpaulensis* Brakoniecki, 1984, collected in a bottom trawl survey off Rio Grande do Sul, Brazil, in 1983 (see Haimovici and Andriguetto Jr., 1986). *L. brasiliensis* Blainville, 1823, was the name most commonly applied to the common loliginid in Brazilian waters in the majority of papers published in South America (e.g. Castellanos, 1967; Juanicó, 1980; Figueiras and Sicardi, 1980; Vigliano, 1985). Brakoniecki (1984) considered *L. brasiliensis* a *nomen dubium*, since the holotype no longer exists and because the original description was inadequate and could refer to any of the species of Loliginidae of the Southwest Atlantic (see also Voss, 1974).

Eighty-six specimens were measured within two hours of capture. Then, 40 specimens were frozen, 20 fixed in 10% buffered formalin in sea water and 26 fixed in 70% ethanol. The frozen individuals were thawed and measured again

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Table 1. Methods and length of treatments of *Loligo sanpaulensis*.

Treatment	Number of animals	Mantle length range (mm)	Length of treatment Short-term (days)	Length of treatment Long-term (months)
10% Formalin	20	36-104	55	46
70% Ethanol	26	38-112	50	46
Freezing	40	52-88	40	46
Freezing; then 10% formalin	20	52-79	40-40	46
Freezing; then 70% ethanol	20	60-88	40-40	46

after 40 days. Half were transferred to 10% formalin and half to 70% ethanol. All measurements were repeated after 46 months of preservation in the corresponding fixatives (Table 1). These procedures can be considered fixation and preservation techniques as defined by Roper and Sweeney (1983).

Measurements taken were: 1, mantle length (ML); 2, fin length (FL), from posterior mantle tip diagonally to the insertion of anterior left border; 3, fin width (FW); 4, arm length (AL), length of third left arm, measured from its tip to the anterior margin of left eye; 5, length of extended left tentacle (TL), measured as for the arm; 6, eye diameter (ED). Measurements 1, 3 and 6 follow Roper and Voss (1983). The corresponding indices were calculated as percentages of the mantle length, e.g. TLI, ALI, FLI, FWI, EDI (Roper and Voss, 1983).

COMPARISONS BEFORE AND AFTER TREATMENTS

Ratios of measurements and indices before and after fixation, and after almost 4 years of preservation are shown in figure 1. Values of 1.0 indicate no change, higher values indicate distension and lower values indicate contraction. Ninety-five-percent confidence intervals were calculated and Student's "t" tests were performed to show significant differences between rate values and the value of one.

Fixation in formalin increased FW, FWI and FLI, and reduced TL and TLI. Formalin preservation reduced FL, TL and TLI. Fixation and preservation in ethanol reduced all measurements and indices, except FL and FLI for fixation, and AL, ALI and FLI for preservation.

Freezing reduced mantle and fin length, and increased the other measurements. Posterior fixation in ethanol or formalin reduced significantly all measurements. The only index reduced was FWI, after freezing/formalin fixation. Further changes occurred for all indices after long-term preservation.

COMPARISONS AMONG TREATMENTS

Growth of *Loligo sanpaulensis* within mantle length ranges of our samples was shown to be allometric by Vigliano (1985) and for other loliginids by Haefner (1964). Indices prior to treatments were observed to be heterogeneous between lots. In order to overcome these constraints, differences between indices before and after each treatment were calculated and covariance analysis (ANCOVA) was applied to the new sets of variables using ML as covariate. Adjusted means and 95% confidence intervals were determined by the GT2 method, using the modification of Gabriel (Sokal and Rohlf, 1981). The overlap of confidence intervals between any pair of treatments indicated whether or not they operate in significantly different ways (Fig. 2).

Differences were found in FWI and EDI between the groups placed directly into formalin vs. alcohol. Arm length index, TLI and FLI of the lot fixed in ethanol differed from the frozen and ethanol fixed lot. Fin length index, TLI and FWI of the lot directly fixed in formalin differed from the previously frozen one. Only formalin fixation following freezing and ethanol fixation following freezing did not show significant differences in any of the calculated indices.

Except for tentacle and arm indices, most differences between treatments were no more observed after long-term preservation. No differences were detected between animals preserved in formalin and in ethanol, as well as between those previously frozen. However, material fixed and preserved directly in ethanol was different from that preserved following freezing in terms of ALI and TLI, and specimens fixed and preserved directly in formalin differed from those previously frozen in their indices of arm length, tentacle length and eye diameter.

DISCUSSION

Many teuthologists have expressed concern about the validity of comparing measurements and morphometric indices of specimens of Loliginidae subjected to different fixation and preservation procedures (Haefner, 1964; LaRoe, 1967; Cohen, 1976; Hixon *et al.*, 1981). Haefner (1964) found arms and tentacles to shrink more than 5% in *Loligo pealei* Lesueur, 1821 and *Lolliguncula brevis* (Blainville, 1823) preserved in 5% formalin, and showed that growth of those species is allometric, indicating that it is imprudent to compare indices from groups having different sizes. LaRoe (1967) observed a contraction of 1.3% in ML of 15 specimens of *Doryteuthis plei* (Blainville, 1823) fixed in 10% formalin and preserved in 70% ethanol. Hixon *et al.* (1981) point out an approximate 5% shrinkage for *Loligo pealei* fixed in 10% formalin and later transferred to 55% isopropanol.

As far as we know, only Cohen (1976) compared body proportions in specimens submitted to different fixation procedures. She found differences in the adjusted means of ANCOVA performed with ML as covariate for *Loligo pealei*

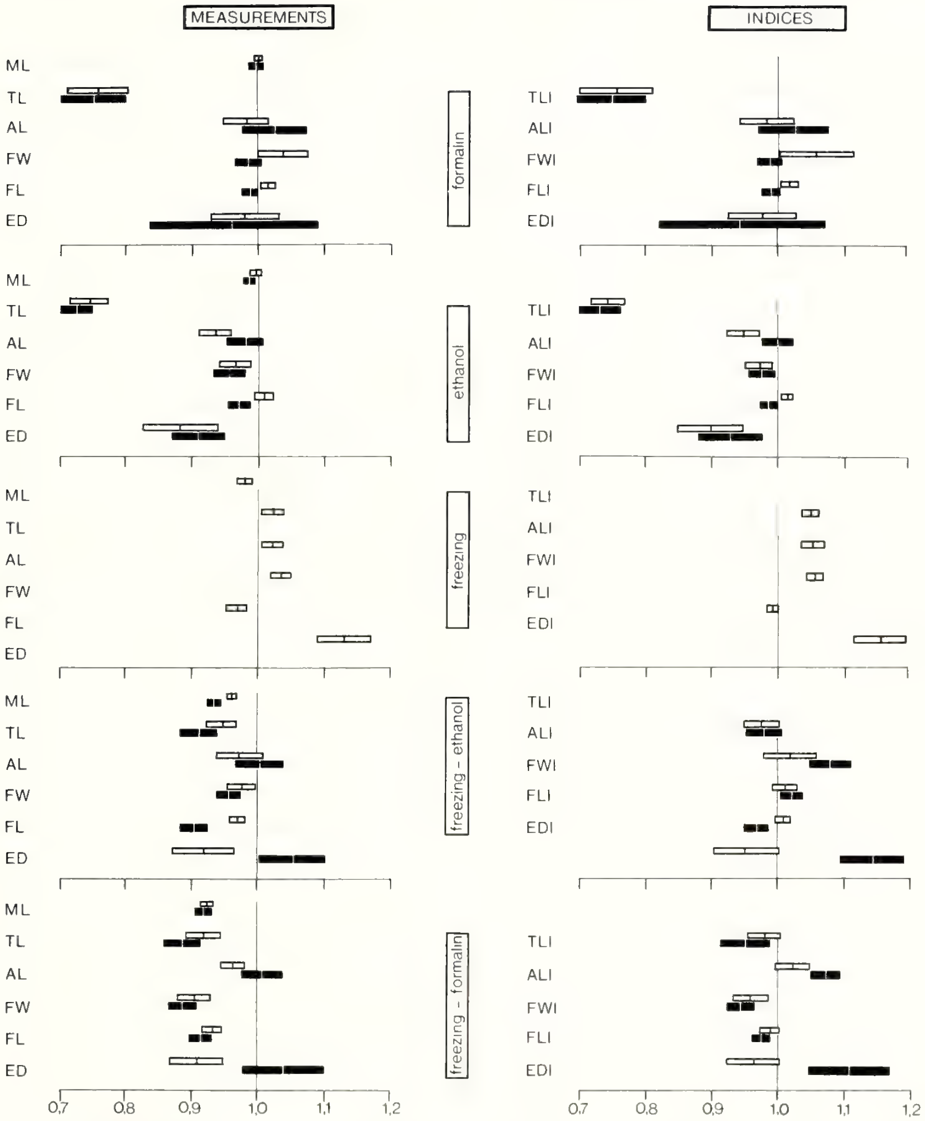

Fig. 1. Means and 95% confidence intervals of the quotients of measurements and indices by treatments. White bars indicate short-term changes; black bars indicate long-term changes. A change is significant when a confidence interval does not include unity.

fixed in 10% formalin and preserved in 40% isopropyl alcohol, when comparing lots of specimens fixed immediately after capture with those previously refrigerated for 48 hours.

Our experiment included other treatments and periods than those tested by Cohen. In addition, we compared changes rather than absolute differences in measurements and indices between lots. This enabled us to compare heterogeneous lots.

Refrigeration and freezing are common methods for stocking squids in commercial fishing, and are useful if fixatives, such as formalin are forbidden on board. The results of Cohen (1976) and those presented here show that some indices in previously refrigerated or frozen specimens are not comparable with those of directly fixed ones, even if the same chemicals were used. The same applies to preservation in ethanol and formalin for several years, although to a lesser degree.

Long-term preservation effects increased the mean variance of indices and consequently the width of confidence limits, making the discrimination of real differences from preservation artifacts more difficult. Despite the small number of indices included in our analysis, the results show that numerical comparisons of populations or species of loliginids based on body dimensions and proportions should consider fixation and preservation induced artifacts, if lots were treated in different ways. The measurement of just caught, fresh specimens, or the comparison of lots fixed and preserved in the same way for similar periods is advisable, unless effects of specific treatments on indices are previously known.

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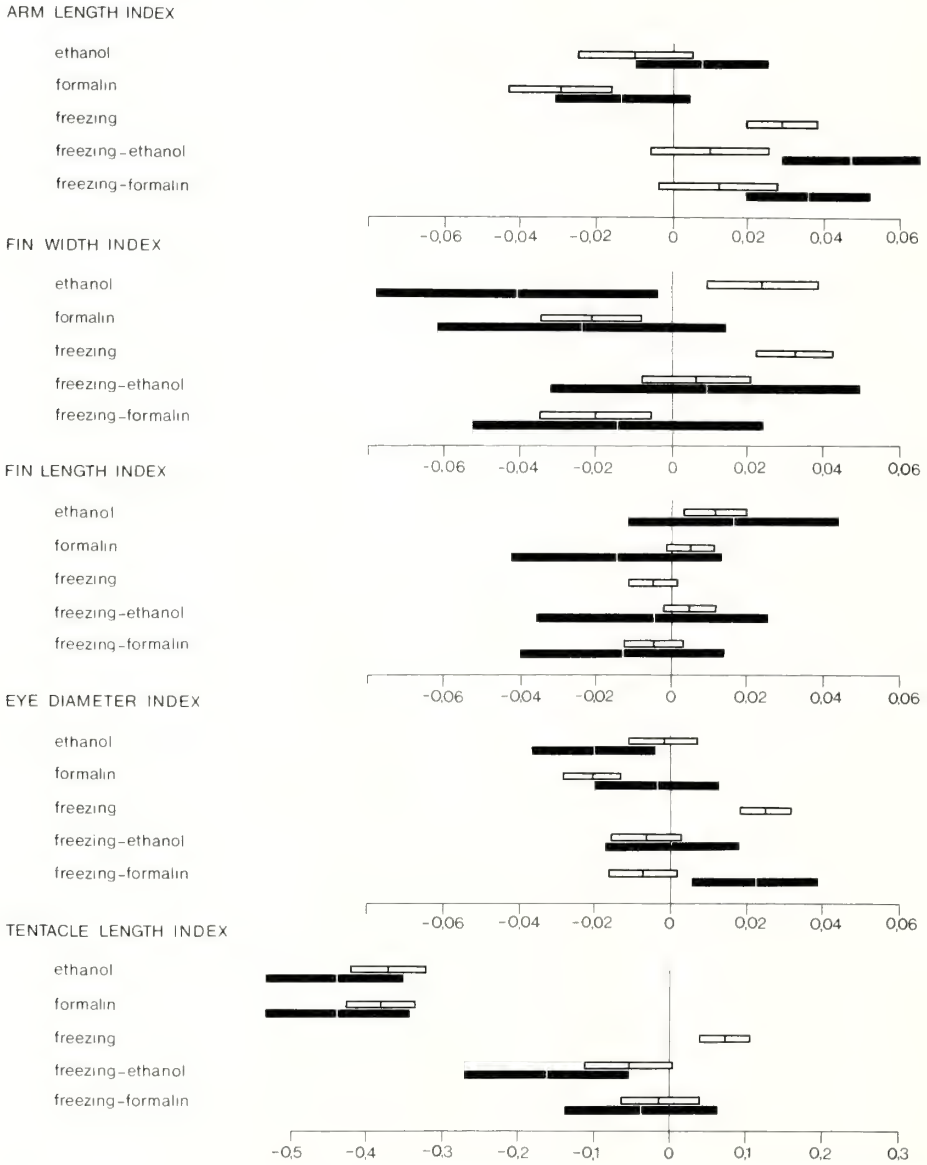

Fig. 2. Adjusted means and 95% confidence intervals of differences between morphometric indices before and after each treatment. White bars indicate short-term differences; black barks indicate long-term differences. Treatments differ significantly when their confidence intervals do not overlap.

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INDEX TO THE AMERICAN MALACOLOGICAL BULLETIN: 1983 TO 1988

VOLUMES 1 THROUGH 6, SPECIAL EDITION NUMBERS 1-3

CLEMENT L. COUNTS, III

Coastal Ecology Research Laboratory
University of Maryland Eastern Shore
Princess Anne, Maryland 21853, U.S.A.

With the appearance of Volume 6, No. 2, the *American Malacological Bulletin* completes its first six years of publication. The *Bulletin* succeeded the *Bulletin of the American Malacological Union* in 1982 when it was recognized that an expanded format was necessary to communicate the proceedings of the annual meetings of the American Malacological Union in a reviewed format as well as to provide an outlet for malacological research not necessarily presented at A.M.U. meetings. Since the appearance of Volume 1 in 1983, the *American Malacological Bulletin* has published nine issues totaling 1,161 pages of primary research articles (111 papers with a total of 1061 pages and 310 research abstracts with a total of 100 pages). Also, during the first six years, the *Bulletin* has published three Special Editions comprising 47 research papers (428 pages) and 1 abstract (1 page). Thus, the *Bulletin* has published 158 papers and 311 abstracts for a total of 1,590 pages during its first six years.

Because of this expanded publication format, it was felt that an index to the first six volumes and three special publications was necessary to increase their usefulness as a malacological research resource. Accordingly, the following index was assembled to include authors, taxonomic groups, geographic localities, and various major subject headings. Each major category is provided as a separate index.

DATES OF PUBLICATION AND KEY

The following is a compilation of the dates of publication of the first six volumes of the *American Malacological Bulletin* and the first three Special Editions. The abbreviations for volume and issue numbers are in brackets following each date of publication. These abbreviations are used throughout the index.

Volume 1: May 1983 [1]
Volume 2: February 1984 [2]
Volume 3, No. 1: December 1984 [3(1)]
Volume 3, No. 2: June 1985 [3(2)]
Volume 4, No. 1: February 1986 [4(1)]
Volume 4, No. 2: August 1986 [4(2)]
Volume 5, No. 1: January 1987 [5(1)]
Volume 5, No. 2: June 1987 [5(2)]
Volume 6, No. 1: January 1988 [6(1)]
Volume 6, No. 2: July 1988 [6(2)]
Special Edition No. 1: July 1985 [S1]
Special Edition No. 2: June 1986 [S2]
Special Edition No. 3: October 1986 [S3]

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Corbicula fluminea: S2:7-39

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Lake Eorom, Denmark
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Lake Fairfield, TX
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Lake Hwama, PRC
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Lake Jackson, FL
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Lake Jennings, CA
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Lake Keowee, SC
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Lake Long, TX
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- Pound Creek, GA
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- Powell River, TN
  - *Actinonaias ligamentina, A. ligamentina gibba, A. pectorosa, Alasmidonta marginata, Amblema plicata, Cumberlandia monodonta, Cyclonaias tuberculata tuberculata, Cyprogenia stegaria, Dromus dromas dromas, D. dromas caperatus, Elliptio crassidens, E. dilatata, Epioblasma brevidens, E. capsaeformis, E. haysiana, E. lewisi, E. torulosa gubernaculum, E. triquetra, Fusconaia barnesiana, F. barnesiana bigbyensis, F. cor., F. cor analoga, F. cuneolus cuneolus, F. subrotunda, F. subrotunda lesuerianus, Hemistena lata, Lampsilis cardium, L. fasciola, L. ovata, Lasmigona costata, L. holstonia, Lemiox rimosa, Leptodea fragilis, Lexingtonia dolabelloides, Ligumia recta, L. recta latissima, Medionidus conradicus, Plethobasus cyphyus, Pleurobema oviforme, P. oviforme argenteum, Potamilus alatus, Ptychobranchus fasciolare, P. subtentum, Quadrula cylindrica cylindrica, Q. cylindrica strigulata, Q. intermedia, Q. pustulosa, Q. sparsa, Strophitus undulatus, Toxolasma lividus lividus:* 6(1):19-37. Unionids, unspecified: 1:93-94. *Villosa fabalis, V. iris, V. vanuxemensis:* 6(1):19-37
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- Preston Rockshelter, WI
  - *Amblema plicata, Anodonta grandis, Anodontoides ferrussacianus, Elliptio dilatata, E. dilatatus delicatus, Lampsilis radiata luteola, L. ventricosa, Lasmigona complanata, Potamilus alatus:* 5(2):165-171
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  - *Acanthochitona woodwardi, Chiton peregrinus, C. (Rhyssoplax) affinis, Ischnochiton winckworthi, I. yerbury, Lepidozona luzonica, Notoplax (Notoplax) arabica, Pinna muricata, Tonicia (Lucilina) sueziensis:* 6(1):115-130
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  - *Berthella pellucida, Euselenops luniceps,* Moreton Bay, *Pleurobranchus peronii:* 5(2):197-214
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  - *Corbicula fluminea:* S2:7-39
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- Reelfoot Lake, TN
  - *Amblema plicata, Anodonta grandis, A. grandis corpulenta, A. imbecilis, A. suborbiculata, Arcidens confragosus, Lampsilis siliquoidea, Leptodea fragilis, Ligumia subrostrata, Megalonaias nervosa, Plectomaris dombeyanus, Quadrula pustulosa, Q. quadrula, Toxolasma parva, T. texasensis, Truncilla truncata:* 6(1):19-37
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  - *Amnicola limosa:* 5(1):9-19. *Arctica islandica,* Block Island: S3:51-57. *Campeloma decisum, Cipangopaludina chinensis:* 5(1):9-19. *Crepidula convexa, C. plana:* 4(2):173-183. *Ferrissia fragilis, F. parallela, Gyraulus circumstriatus, G. deflectus, G. parvus, Helisoma anceps, H. campanulatum, H. trivolvis, Laevapex fuscus, Lyrogyrus granum, L. pupoidea:* 5(1):9-19. *Margaritifera margaritiferae:* 4(1):13-19. *Micromentus dilatatus, Physa ancillaria, P. heterostropha, Planorbula armigera, Promenetus exacuous, Pseudosuccinea columella, Stagnicola elodes, Valvata tricarinata, Viviparus georgianus:* 5(1):9-19
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  - *Anodonta imbecilis henryiana, A. grandis:* 2:86. *Corbicula fluminea:* 2:86; S2:7-39. *Cyrtonaias tampicoensis berlandieri, Disconaia salinasensis, Lampsilis teres, Megalonaias gigantea, Popenaias popei, Quadrula apiculata, Toxolasma parvus, Uniomerus tetralasmus manubius:* 2:86
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- Roanoke River, NC
  - *Anodonta implicata, Corbicula fluminea, Elliptio complanata:* 3(1):104-105
- Roaring River, TN
  - *Anodontoides ferussacianus, Lampsilis fasciola, Lasmigona costata, Medionidus conradicus, Toxolasma lividus glans, Villosa taeniata picta, V. taeniata punctuata:* 6(1):19-37
- Roatan, Honduras
  - *Acanthochiles (Notoplax) hemphilli,* Anthony Keys, *Choneplax lata,* Oak Ridge: 6(1):79-114
- Rockcastle River, TN
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  - *Corbicula fluminea:* S2:7-39
- Rocky River, NC
  - *Corbicula fluminea:* S2:7-39
- Roosevelt Lake, AZ
  - *Corbicula fluminea, Ictiobus bubalus, I. cyprinellus, I. niger:* S2:7-39
- Russian River, CA
  - *Corbicula fluminea:* S2:7-39
- Rutherford Creek, TN
  - *Corbicula fluminea:* S2:7-39
- Sabine River, LA, TX
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- St. Andrews Bay, FL
  - *Acanthochitona pygmaea:* 6(1):79-114
- St. Croix River, MN, WI
  - *Corbicula:* S2:1-5. *C. fluminea:* S2:7-39
- St. Eustatius
  - *Acanthochiton balesae,* Tumble Down Dick Bay: 6(1):79-114
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  - *Corbicula fluminea:* S2:7-39
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  - *Corbicula fluminea:* S2:7-39. *Elliptio productus:* 3(1):94
- St. Joseph Bay, FL
  - *Corbicula fluminea:* S2:7-39. *Halodule wrightii, Laurencia poitei, Marginella aureocincta, Rissoina catesbyana, Thalassia testudinum:* 4(2):185-199
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  - *Cerithidea obtusa,* Miocene: 2:1-20
- Salinas River, CA
  - *Corbicula fluminea:* S2:7-39
- Saline River, AR
  - *Corbicula fluminea:* S2:7-39
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- Salkahatchie River, SC
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- Salt Creek, IN
  - *Corbicula fluminea:* S2:7-39
- Salt Pond, Bahama Islands
  - *Acanthochitona zebra:* 6(1):79-114
- Salt River, AZ
  - *Corbicula fluminea:* S2:7-39
- Salt River, KY
  - *Corbicula fluminea:* S2:7-39
- Salton Sea, CA
  - *Corbicula fluminea:* S2:7-39
- San Antonio, TX
  - *Corbicula fluminea:* S2:7-39
- San Diego City Waterworks, CA
  - *Corbicula fluminea:* S2:7-39
- San Francisco Bay, CA
  - *Boccardia ligerica:* S2:7-39. *Cerithidea californica:* 2:1-20. *Corbicula fluminea, Corphium spinicoine, C. stimpsoni, Macoma balthica:* S2:7-39
- San Gabriel River, TX
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  - *Amiantus* sp., *Calliostoma hannibali, Chione (Chione) richthofeni, C. (Chionopsis)* sp., *Choromytilus palliopunctatus, Crassilabrum wittichi, Crassispira starri, Crepidula* sp., *Crucibulum inerme, C. scutellatum, Cyclinellas, Cymia heimi, Cypraea amandusi, Divalinga comis, Drillia (Clathrodrillia)* sp., *Knefastia* sp., *Lucina (Lucinisca)* sp., *Macron hartmani, Mytilus canoasensis vidali, Nassarius versicolor, Nerita funiculata, Neverita (Glossaulax) andersoni, Ostrea* sp., Paleontology, *Sanguinolaria toulai, Solenosteira* sp., *Strombina* sp., *Terebra burckhardti, Trachycardium* sp., *Turritella bosei, T. costaricensis:* 4(1):1-12
- San Jacinto Reservoir, CA
  - *Corbicula fluminea:* S2:7-39
- San Jacinto River, TX
  - *Corbicula fluminea:* S2:7-39

- San Joaquin River, CA
  - *Corbicula fluminea:* S2:7-39, 133-142
- San Juan Island, WA
  - *Lepidochitona, L. dentiens:* 4(2):243
- San Luis Reservoir, CA
  - *Corbicula fluminea:* S2:7-39
- San Nicolas Island, CA
  - *Micrarionta opuntia:* 3(1):98; 4(2):237. *M. sodalis:* 3(1):98; 4(2):237
- San-Men-Hsia Reservoir, PRC
  - *Corbicula nitens:* S2:113-124
- Sand Key, FL
  - *Acanthochiles (Notoplax) hemphilli:* 6(1):79-114
- Sandy Creek, MI
  - *Corbicula fluminea:* S2:7-39
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  - *Corbicula fluminea:* S2:7-39
- Sanibel Island, FL
  - *Acanthochitona pygmaea:* 6(1):79-114. *Anomia simplex, Argopecten gibbus, Chione cancellata:* 2:41-50
- Santa Anna River, CA
  - *Corbicula fluminea:* S2:7-39
- Santa Barbara Channel, CA
  - *Cuthona albocrusta, Eubranchus, Hermissenda crassicornis:* 5(2):287-292
- Santa Barbara Harbor, CA
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- Santa Bouge Creek, AL
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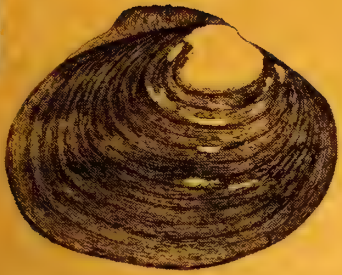

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and State University
Blacksburg, Virginia, U.S.A.

JAMES W. NYBAKKEN
Moss Landing Marine Laboratories
Moss Landing, California 95039-0223

WINSTON F. PONDER
Australian Museum
Sydney, Australia

CLYDE F. E. ROPER
U.S. National Museum
Washington, D.C., U.S.A.

NORMAN W. RUNHAM
University College of North Wales
Bangor, United Kingdom

AMELIE SCHELTEMA
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts, U.S.A.

ALAN SOLEM
Field Museum of Natural History
Chicago, Illinois, U.S.A.

DAVID H. STANSBERY
Ohio State University
Columbus, Ohio, U.S.A.

FRED G. THOMPSON
University of Florida
Gainesville, Florida, U.S.A.

THOMAS E. THOMPSON
University of Bristol
Bristol, United Kingdom

NORMITSU WATABE
University of South Carolina
Columbia, South Carolina, U.S.A.

KARL M. WILBUR
Duke University
Durham, North Carolina, U.S.A.

Cover. Mantle cavity organs of *Batissa violacea* (Lamarck, 1797), the right valve of which is seen here in lateral view, are discussed in an article by Morton in this volume, pages 73-80.

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CAMPANILE REVISITED: IMPLICATIONS FOR CERITHIOIDEAN PHYLOGENY

RICHARD S. HOUBRICK
DEPARTMENT OF INVERTEBRATE ZOOLOGY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D. C. 20560, U. S. A.

ABSTRACT

Aspects of the anatomy of *Campanile symbolicum* Iredale, the sole survivor of the large campanilid lineage, are reexamined and compared with data derived from past and recent studies of this aberrant gastropod. These data provide evidence to support a new systematic placement of *Campanile* at the base of, but outside the Cerithioidean clade. The family Campanilidae, is herein raised to superfamilial rank, Campaniloidea Douville, 1904, and is regarded as an early, major radiation off the stem that gave rise to Cerithioidea and Caenogastropoda.

The abberant, relictual taxon, *Campanile symbolicum* Iredale, 1917, stands apart from all other Recent Caenogastropoda by many unusual conchological and anatomical features. These were first noted in an anatomical and systematic study in which aspects of the ecology and reproductive biology of this marine gastropod were also represented (Houbrick, 1981). The paleontology and radiation of the family Campanilidae Douville, 1904 were also described and the taxonomy of the group outlined.

The Campanilidae was a large, diverse, complex group, that attained its apogee during the early Tertiary, and is best known from the Paris Basin Eocene fauna. The campanilid radiation was extensive and comprised diverse genera and numerous species. Fossils are known from the Indo-Pacific and western Atlantic, as well as from many European Tethyan sites, where the group was particularly diverse (Houbrick, 1981). Some taxa attained sizes of up to a meter in length, and several Caribbean Eocene *Campanile* fossils of even greater lengths, have been recently described and illustrated (Jung, 1987).

The salient characters defining the sole living representative of the group, *Campanile symbolicum,* were recently summarized and a cladogram illustrating its position relative to other cerithioidea taxa was presented (Houbrick, 1988:115, fig. 2). Since that work, new studies on prosobranch phylogeny, that include other aspects of *Campanile* anatomy (Haszprunar, 1985; 1988; Salvini-Plawen and Haszprunar, 1987; and Houbrick, 1988), and comprehensive ultrastructural studies of its spermatozoa (Healy, 1983; 1986a, b), have been published. These studies examined specific anatomical traits in more detail, and have provided new characters and additional data enhancing our understanding of the systematic placement of this strange gastropod.

An opportunity to restudy living *Campanile* specimens in Albany, Western Australia, allowed me to check my previous work (Houbrick, 1981) for accuracy as well as to make several new observations. The original study (Houbrick, 1981) was conducted during the Australian winter, while the present one was made in the summer of 1988 (Jan). The new study and data from recently published findings of the above mentioned authors, reinforce the concept that *Campanile* is indeed an aberrant gastropod, difficult to place within the framework of conventional molluscan systematics. Reevaluation of the original findings, additional data compiled from the recent literature, and new anatomical information obtained from the present investigation, all indicate that the phylogenetic relationship of the family Campanilidae to the superfamily Cerithioidea is in need of critical examination and reassessment, and have prompted this paper.

MATERIALS AND METHODS

Live specimens of *Campanile symbolicum* Iredale, 1917, were collected in Princess Royal Harbour, Albany, Western Australia, in shallow water amongst rocks and sand associated with *Possidonia* grass beds, during January, 1988. Shells were cracked with a vice, and the animals extracted and relaxed in a 7.5% $MgCl_2$ solution isotonic with seawater prior to dissection. Radulae and tissues prepared for critical point drying were examined with an Hitachi S-570 Scanning Electron

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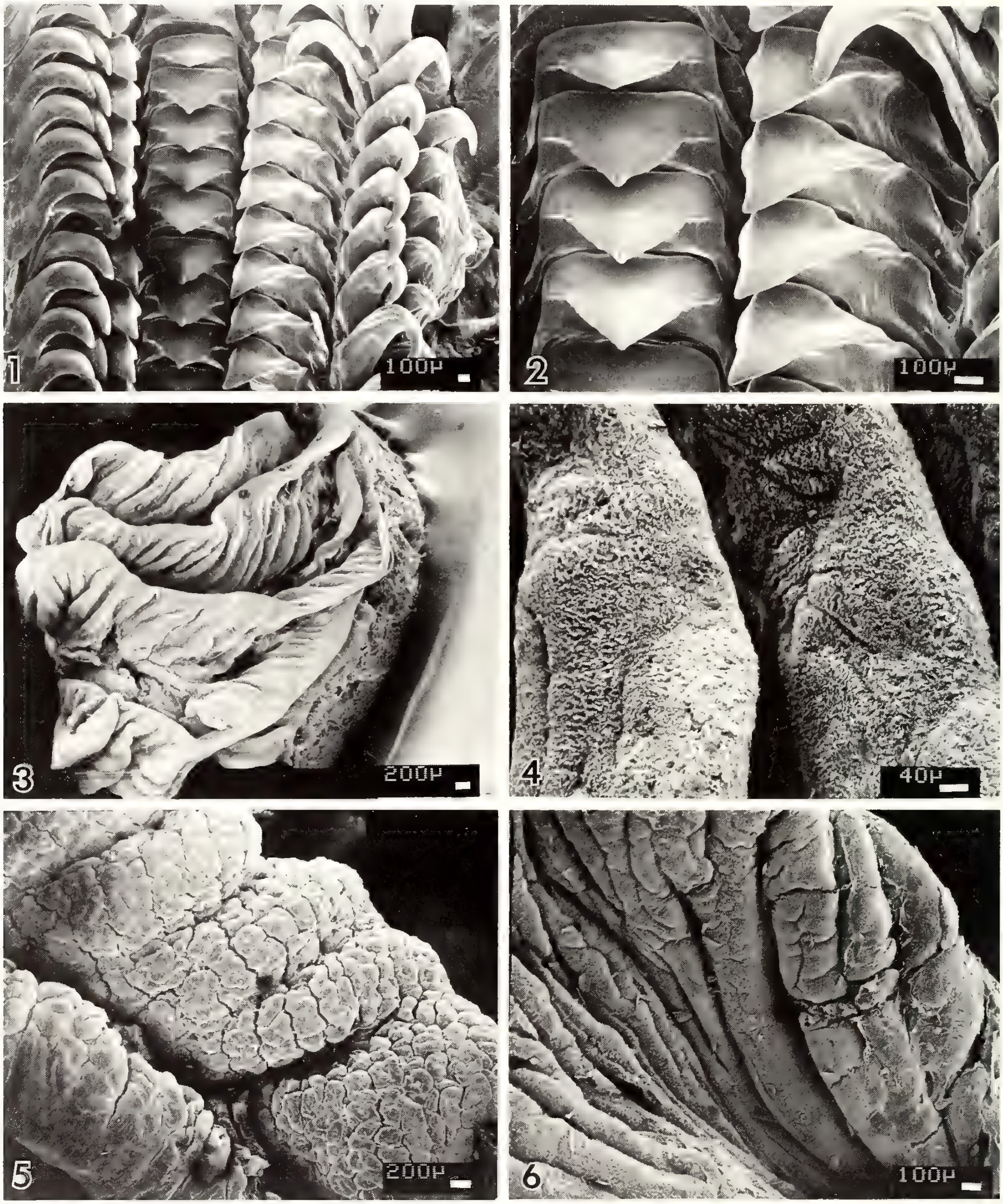
Microscope (Figs. 1-6). The egg mass was photographed under a Wild M-5 dissecting microscope (Figs. 7-8). Material for histological examination was fixed in Bouin's fixative, embedded in paraffin, and sectioned at 5 μm. Sections were stained in Mallory's Triple Stain (Figs. 9-10). The characters derived from this study were compared with my cladogram on cerithioidean phylogeny (see Houbrick, 1988, Fig. 2) for congruence and used as an independent test of my original conclusions about the placement of *Campanile*. Voucher specimens from Albany, Western Australia (USNM 867015), have been deposited in the National Museum of Natural History, Smithsonian Institution.



Figs. 1-6. Scanning electron micrographs of *Campanile symbolicum* anatomy (all USNM 867015, Princess Royal Harbour, Albany, West Australia). **Fig. 1.** Radula with right marginal teeth spread back. **Fig. 2.** Detailed view of rachidian and lateral teeth. **Fig. 3.** Spirally arranged leaflets removed from anterior liver duct. **Fig. 4.** Detail of ribs on liver duct leaflet showing ciliated epithelium. **Fig. 5.** Detail of surface of pad-like fold emerging from spiral caecum, showing densely packed papillae. **Fig. 6.** Ciliated folds of anterior hypobranchial gland.

RESULTS

The basic anatomy of *Campanile symbolicum* has been set forth in a previous paper (Houbrick, 1981) and these original findings verified by dissections made during this study. New comments clarifying past descriptions, several corrections, and new anatomical observations follow.

The arrangement of the dark brown digestive gland and light colored gonad in the visceral whorls of *Campanile* is unusual. The wide gonad (? ovotestis) is sharply demarcated from the digestive gland on the peripheral surface of the external anterior visceral whorls, exclusive of the kidney and stomach, presenting a banded appearance not normally seen in other prosobranchs. In addition, the gonad appears to be dispersed throughout the interior of the digestive gland.

One of the more interesting and unusual features of *Campanile* is the alimentary system, which has features that are unique among Caenogastropoda. Deep epithelial folds line the lips, and the thick, four-layered ultrastructure of the large, stout jaws (see Houbrick, 1981:274, fig. 2d,e) does not occur among other cerithioideans, or as far as is known, among other prosobranchs. As pointed out previously (Houbrick, 1981:274-275), the radular ribbon (Fig. 1) is very wide and robust, but unusually short for so large an animal, attaining a length only about 8% of the shell length. The rachidian tooth is notable in having a very large, broad, central cusp with only weak traces of minor denticles (Fig. 2). The lateral teeth are similar but have a small inner denticle (Fig. 2). The interior buccal cavity is lined with deeply folded, glandular tissue, which greatly increases its surface area. The large, so-called esophageal pouches are unusual structures and it is doubtful that they are homologous with the esophageal pouches described by Fretter and Graham (1962:26) in *Littorina*; hence, my hesitation in using the same name for these structures. In *Campanile*, the pouches differ from those of *Littorina* in being more internally complex and highly muscular, in having a short, narrow, highly constricted connection to the buccal cavity, and in being lined with thick, dark-staining glandular tissue of unknown function (Houbrick, 1981:275, fig. 7f). The salivary glands are tiny relative to the size of the snail, and are located well anterior to the nerve ring. The existence of a muscular, transverse septum behind the nerve ring, completely dividing the cephalic haemocoel between the anterior esophagus and the mid-esophagus, is confirmed. As noted previously (Houbrick, 1981:275), a transverse septum is known only in trochaceans (archaeogastropods), but not in caenogastropods. The mid-esophagus of *Campanile* is highly unusual in that it is surrounded by a thick layer of very loose connective tissue which is in turn surrounded by a thin layer of muscular tissue (see Houbrick, 1981:275, fig. 7e).

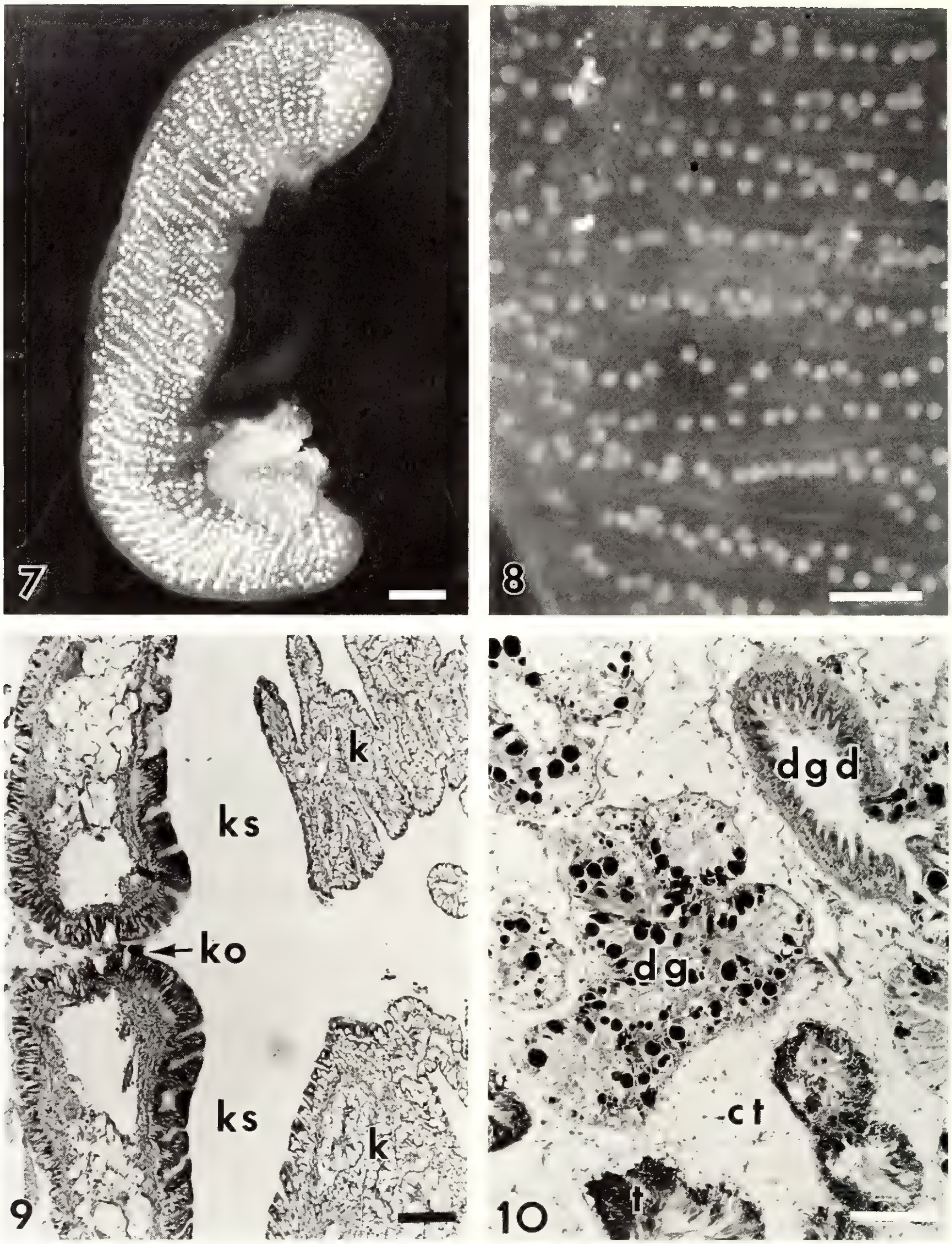
The morphology of the large stomach of *Campanile*, one of its strangest features, sets it apart from those of all other caenogastropods. The drawing of the stomach presented by Houbrick (1981:fig. 5b) is essentially accurate, but a few points need clarification: 1) The fold emerging from the spiral caecum (*ff* on drawing) is a large pad-like structure comprised of densely packed papillae having a ciliated surface (Fig. 5); 2) The so-called gastric shield in the drawing (*gs*) is not a gastric shield, but a raised, ciliated pad adjacent to the large fold (*ff*) and to the sorting area; 3) The grooved sorting area in the drawing (*gsa*) is cuticularized, and is probably homologous to the cuticularized part of the anterior chamber and perhaps the gastric shield of other caenogastropods; 4) There are two openings (ducts) into the anterior lobe of the digestive gland rather than one, and contrary to the original description (Houbrick, 1981:276), the so-called "pit" with spirally arranged leaflets is not blind, but branches deeply into the digestive gland. Both openings are large, and the unusual spirally arranged leaflets comprising the anterior digestive gland duct branch deeply into the far anterior lobe of the digestive gland. The illustration of these leaflets in the original description (Houbrick, 1981:276, fig. 5, sl) was inadequate, and is here augmented by scanning electron micrographs (Figs. 3-4). The leaflets are largest at the conical shaped opening to the digestive gland and become progressively smaller as they spiral downward. Each of the leaflets is transversely ribbed, presenting a veined appearance and is entirely covered with small cilia (Fig. 4); 5) Although a shallow, rudimentary style sac is present, there is a raised cuticular area posterior to the style sac instead of a conventional gastric shield and the crystalline style is absent. The stomachs of freshly taken snails showed no trace of a crystalline style: only a short protostyle (*sensu* Morton, 1967:112) was present.

The digestive gland is very large, comprising 4-5 whorls, and is a very dark color due to the great numbers of deep brown concretions (Fig. 10, dg), which are found in the basal parts of the cells and which loosen and fall out when the gland is cut, and darkly stain preserving fluids.

The large, saddle-shaped, dark tan kidney is a conspicuous external feature of the animal. There are two main parts to the kidney: an elongate, solid section, comprised of many fine lamellae (Fig. 9, k), covers the pericardium dorsally and posteriorly and extends posteriorly to overlie the posterior gonoduct and posterior mantle cavity; it has a spacious anterior cavity or kidney sac (Fig. 9, ks), adjacent to the kidney opening (Fig. 9, ko); the other part of the kidney, of looser, spongy consistency due to larger lamellae and numerous lumina, is seen in section to be filled with tiny excretory granules; it is adjacent to and surrounds the anterior stomach. This was not identified as a separate part of the kidney in the original description (Houbrick, 1981:276). A third, lighter pigmented part of the kidney, thought to be the nephridial gland (Houbrick, 1981:276), borders the pericardial sac, but histologically does not appear to consist of different tissue than that of the main kidney.

DISCUSSION

Although the large, well-developed, bipectinate osphradium of *Campanile* is similar to those of rachiglossate, predatory neogastropods, herbivory has been reconfirmed. Stomach contents and a large food bolus taken from the anterior liver duct consisted of large pieces of *Possidonia* seagrass as well as coarse fragments of foliated and articulated algae, which were primarily *Cladophora*, but also



Figs. 7-10. *Campanile symbolicum* (USNM 867015). **Fig. 7.** Egg mass length 120 mm (bar = 11 mm). **Fig. 8.** Detail of egg mass showing fine filamentous threads between egg chambers (bar = 0.6 mm). **Fig. 9.** Section through kidney sac showing kidney tissue (k), kidney sac (ks),and kidney opening (ko) to mantle cavity (mc); (bar = 0.25 mm). **Fig. 10.** Section through digestive gland (dg) and testis (t) showing connective tissue (ct) and a duct of the digestive gland (dgd). Dark round objects are digestive gland concretions (bar = 1 mm).

some *Specelaria.* Algal pieces are probably manipulated and compressed by the large pad-like structures in the stomach to form a bolus prior to its movement into the liver ducts. The unusual, large, branched, structure of the interior liver ducts (Fig. 10, dgd) suggests that the bolus of algal fragments is pushed deeply into them. The many unusual features of the alimentary system indicate that the feeding ecology and digestive physiology of *Campanile* would be an interesting study.

In the discussion of my original paper (Houbrick, 1981:283-289) I proposed and justified familial status for *Campanile,* and allocated Campanilidae to the superfamily Cerithioidea; however, I noted that the many unique and unusual anatomical features of the only living representative of the family, *Campanile symbolicum*, do not conform to the normal cerithioidean groundplan (see Houbrick, 1988 for detailed description of Cerithioidea), and that some characters suggest affinities with neogastropods (rachiglossa) and opisthobranchs.

In a recent study of cerithioidean phylogeny (Houbrick, 1988) in which 58 characters comprising 134 character states were used to generate cladograms of 15 cerithioidean families, the Campanilidae consistently fell out at the bases of the various trees generated, irrespective of outgroups used or of interpretations of multistate character polarity. Among all cerithioidean families, Campanilidae was consistently the most primitive taxon and was at the base of the final, most parsimonious cladogram (Houbrick, 1988: fig. 2). Eleven autapomorphies defining the Campanilidae were identified, and it was remarked that *Campanile* would suffice as a good outgroup for all other cerithioidean taxa, and that it occupied an isolated position at the base of the Cerithioidea clade (Houbrick, 1988).

The new characters set forth in this paper reinforce the basal position of *Campanile* on the original cladogram (Houbrick, 1988: fig. 2). Comprehensive studies of the euspermatozoa and paraspermatozoa of *Campanile symbolicum* by Healy (1983, 1986a, 1986b) indicate that major, significant differences exist between spermatozoa of the Campanilidae and other cerithioidean taxa, confirming its unique status among prosobranchs. The nucleus of the euspermatozoon of *Campanile* is three times the length of euspermatozoan nuclei of all other investigated cerithioideans. Although the basic structure of *Campanile* euspermatozoa resembles that of many other mesogastropods, the midpiece region exhibits unusual and possibly unique features (see Healy, 1986b:213). In addition, *Campanile* differs from all other cerithioidean taxa studied in having two types of paraspermatozoa, both with a head (acrosome-like structure) and 2-3 tails. These two types of paraspermatozoa are nucleate, and non-nucleate (Healy, 1986b:207-209). Despite these significant differences, Healy (1986b:214-216) pointed out that *Campanile* paraspermatozoa also share a number of important features with those of the Cerithiidae, Potamididae, Turritellidae, and Planaxidae, and that in many respects the anatomy and sperm morphology of *Campanile* bridge the gap between the Cerithioidea and the remainder of the Caenogastropoda. He concluded that sperm morphology indicates that the Campanilidae occupy an isolated position within the Cerithioidea and that they probably diverged at an early stage from the primitive cerithioidean stock in which sperm dimorphism was established. Healy's (1986b) position was adopted by Ponder and Waren (1988), who considered *Campanile* to be an aberrant cerithioidean.

Haszprunar (1985:24) called attention to the fact that within the Prosobranchia, only *Valvata* and *Campanile* have chalazae. Salvini-Plawen and Haszprunar (1987:762, fig. 4) allocated the Campanilidae to the Caenogastropoda, but as *incertae sedis*, and suggested that the group is a "subsequent offshoot of intermediate grade" between the Caenogastropoda and Allogastropoda (*sensu* Haszprunar, 1984). Thus, they considered Campanilidae to be distinct from and not directly ancestral to Cerithioidea, and suggested that Campanilidae is an intermediate group of caenogastropods sharing some characters with euthyneurans, which they called "Pentaganglionata". Salvini-Plawen and Haszprunar (1987:765) placed emphasis on the presence of chalazae and on the anterior folds (presumed respiratory lamellae) of the hypobranchial gland epithelium as evidence for the transition between the prosobranch and heterobranch grades. The following caveats about this evidence should be noted: 1) In my original paper I mentioned that the string-like connections in *Campanile* spawn masses (see Figs. 7-8), are merely between the mucous capsules forming egg chambers (each containing 1-3 eggs) and not between individual eggs. I pointed out that these connections may not be homologous with the true chalazae of opisthobranch spawn (Houbrick, 1981:285), which join individual eggs; 2) reexamination of the anterior hypobranchial gland casts doubt on its role as a primitive respiratory lamellae. The folds appear to be more poorly defined and less prominent (see Fig. 6) than in my original description (Houbrick, 1981:274, fig. 4, A, *lhg*), and it is doubtful that their function is respiratory.

Haszprunar (1988) recently emphasized that *Campanile* has certain characters of the allogastropod-euthyneuran line; i.e., a genital system with isolated receptaculum, and a gelatinous egg mass with chalazae-connected eggs. In the same paper, he also cited his fine-structural studies of the *Campanile* osphradium (without giving details), which he stated demonstrate a major difference from osphradia of other caenogastropod groups, and which indicate affinities with the Architectonicidae and primitive Euthyneura. Haszprunar (1988) thus concluded that *Campanile* probably represents a first step towards the euthyneurous level of organization. However, Ponder and Waren (1988) pointed out that undoubted fossil opisthobranchs are known from as far back as the Carboniferous, suggesting that euthyneurans arose long before any *Campanile*-like gastropods.

The new observations of *Campanile* anatomy and reanalysis of anatomical characters, plus work on sperm morphology (Healy, 1983; 1986a; 1986b) and on other aspects of *Campanile* anatomy (Haszprunar, 1985; 1988; Salvini-Plawen and Haszprunar, 1987), all confirm the unusual position of Campanilidae relative to Cerithioidea, and Caenogastropoda-Allogastropoda, and perhaps to Euthyneura (Pentaganglionata), and provide evidence arguing for a major reevaluation of its systematic placement.

The Campanilidae should no longer be considered as cerithioidean gastropods. *Campanile* has many notable and significant non-cerithioidean features including: a calcified, pitted periostracum, a complex jaw ultrastructure; buccal pouches; digestive gland openings with spirally arranged leaflets; a transverse septum dividing the cephalic hemocoel from the midesophagus; an unusual arrangement of muscle and connective tissue surrounding the midesophagus; a lamellate albumen gland; a seminal receptacle in both sexes; an isolated, posterior seminal receptacle positioned in the pericardial sac; possible protandry; two kinds of paraspermatozoa; a possibly unique form of the euspermatozoan midpiece; egg chambers linked by chalazae-like strings; lack of hyaline capsules around the eggs; and a short, oval, bipectinate osphradium with unique epithelium. These characters, all of which are autapomorphic among cerithioideans, plus other minor anatomical features, are of sufficient importance and weight to justify removal of *Campanile*, family Campanilidae, from Cerithioidea, and to raise it to superfamilial status (Campaniloidea Douville, 1904). This is contrary to my original classification (Houbrick, 1981:286). A similar view was arrived at independently by Ponder and Waren (1988), who stated that *Campanile* was an aberrant cerithioidean and had little to do with heterobranch evolution.

Salvini-Plawen and Haszprunar (1987) and Haszprunar (1988, in press) have suggested an intermediate, outlying position for Campanilidae between the rest of the Caenogastropoda and the Allogastropoda and Euthyneura, based on three anatomical characters. Two of the so-called euthyneuran features cited for *Campanile* by these authors, chalazae and respiratory folds of the hypobranchial gland, are based on equivocal evidence and are somewhat speculative (see above). The third and possibly best of these characters, the unique osphradial epithelium, is stated to have features in common with Architectonicidae and primitive euthyneurans, but Haszprunar (1988, in press) himself has noted that the osphradium also has several peculiarities of its own, and is unique among Gastropoda. As he does not give details, it is impossible to appraise and judge these osphradial characters. In my opinion, too much significance has been given to the putative euthyneuran characters in Haszprunar's cladogram and resulting classification (1988). Until the ambiguities about the above characters are resolved, less significance and emphasis should be accorded to *Campanile* as a "connecting link" between Caenogastropoda and Euthyneura.

I agree with Haszprunar's (1988) suggestion that the Loxonomatoidea-Cerithioidea stem-group probably gave rise to the Caenogastropoda, and concur that Campanilidae be given superfamily status. However, I believe it best to regard Campaniloidea as an early, major radiation from the mainstream of the stem-group that gave rise to modern Cerithioidea and Caenogastropoda.

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GENETIC CONSEQUENCES OF PARTIAL SELF-FERTILIZATION ON POPULATIONS OF *LIGUUS FASCIATUS* (MOLLUSCA: PULMONATA: BULIMULIDAE)

DAVID M. HILLIS
DEPARTMENT OF ZOOLOGY
THE UNIVERSITY OF TEXAS
AUSTIN, TEXAS 78712, U.S.A.

ABSTRACT

Reproductive modes of the highly polymorphic Florida tree snail, *Liguus fasciatus* (Müller), were investigated by laboratory breeding experiments and field study. Variation of glucose-phosphate isomerase and shell phenotypes was assessed. The laboratory crossings demonstrated that partial self-fertilization does occur in this species, but too few informative crosses were performed to estimate the frequency of self-fertilization. A transect study through two populations that have recently come into contact demonstrated high population substructure ($F_{ST} = 0.437$) across short distances. Levels of heterozygosity in subpopulations along 20 m sections of the transect were used to estimate levels of self-fertilization. Estimates ranged from 46% to 94% self-fertilization, with a mean of 69%. The genotypic frequencies of subpopulations did not differ significantly from expected frequencies assuming the mean estimate of 69% self-fertilization, but did differ significantly from expected frequencies assuming Hardy-Weinberg equilibrium with no self-fertilization. Partial self-fertilization appears to be largely responsible for the low within-population variation compared to the high among-population variation of this species.

Tree snails of the genus *Liguus* are noted for their morphological diversity among populations (Clench, 1946, 1954, 1965; Pilsbry, 1946). In Florida, approximately 58 named varieties of *Liguus fasciatus* (Müller) occur (Roth and Bogan, 1984), many of which are restricted to single tropical hardwood hammocks in the Everglades and Florida Keys (Deisler, 1982). In spite of this high morphological diversity in *L. fasciatus*, allozymic variation is very low among and within populations of this species (Hillis *et al.*, 1987). Furthermore, populations of *L. fasciatus* deviate significantly from Hardy-Weinberg expectations at variable loci because of marked heterozygote deficiencies (Hillis *et al.*, 1987).

Although geographic patterns of phenotypic shell variation have been studied extensively in *Liguus fasciatus* (Pilsbry, 1899, 1912, 1946; Deisler, 1982; Roth and Bogan, 1984), very little is known about the inheritance of these traits or reproduction in this species. Roth and Bogan (1984) proposed a system for describing morphological variation in *L. fasciatus* that consisted of twelve characters, each with two to four states. They stated that they chose characters "...in which the alternate states can be seen to segregate in randomly selected material." However, Hillis *et al.* (1987) suggested that these characters are not independent, and that many fewer than twelve loci are probably responsible for the observed phenotypic variation of shells. Furthermore, although most past authors (e.g. Brown, 1978; Young, 1960) have assumed that *L. fasciatus* is an obligate outcrosser, Hillis *et al.* (1987) suggested that partial self-fertilization might account for some of the patterns of genetic variation seen among populations of this hermaphroditic species. Self-fertilization and outcrossing are both common modes of reproduction in gastropods, and a few species contain some populations that are self-fertilizing and others that are outcrossing (McKracken and Selander, 1980). Other species are facultatively self-fertilizing and self-fertilize when mates are unavailable, and in at least one species reproduction following copulation is either by self-fertilization or outcrossing (McKracken and Selander, 1980). However, partial self-fertilization (a single clutch containing both self-fertilized and outcrossed eggs), as suggested for *L. fasciatus* (Hillis *et al.*, 1987), has not been demonstrated among gastropods.

This study was undertaken to determine the mode of reproduction and its consequences on genetic variation in *Liguus fasciatus*. Laboratory and field studies were designed to determine if partial self-fertilization occurs, and if so, at what frequency. In addition, a population was examined to determine the extent of genetic substructure as well as the effects of possible self-fertilization on heterozygosity, allozymic variation, and phenotypic variation of shells.

MATERIALS AND METHODS

ELECTROPHORETIC METHODS

Standard procedures of horizontal starch gel electrophoresis were followed (Selander *et al.*, 1971; Hillis, 1985). Digestive glands of *Liguus fasciatus* were ground and diluted 1:1 in 0.01 M tris-0.001 M EDTA-.001 M 2-mercaptoethanol, pH 7.5. Homogenates were centrifuged at 7,000 g for 5 min, after which the supernatants were refrozen at -85ºC. A buffer system of 175 mM tris-17.5 mM boric acid-2.75 mM EDTA, pH 9.1 was used. Gels were prepared from 50% Sigma starch (lot 85F-0010) and 50% Otto Hiller electrostarch (lot 392). Gels were electrophoresed for 12 hr at 12.5 V/cm. Histochemical staining for glucose-phosphate isomerase (E.C. 5.3.1.9; GPI) followed Harris and Hopkinson (1976). This enzyme was the only variable locus of the 24 allozyme loci surveyed in *L. fasciatus* by Hillis *et al.* (1987).

BREEDING STUDY

Between 18 January and 5 July 1986, 60 specimens of *Liguus fasciatus* were collected from hammocks in the Pinecrest region, Big Cypress National Preserve, and near Long Pine Key, Everglades National Park, Florida, for captive breeding experiments. Mating in this species begins in late July or early August in these regions (Jones, 1954). Pairs of *L. fasciatus* remain together for several days after mating, so the beginning of the breeding season can be easily ascertained. In summer 1986, the study populations were observed at least twice weekly, and the first mated pairs were found during the first week of August. Therefore, all of the specimens used in the captive breeding study were collected at least one month prior to the breeding season. Specimens from single populations were paired at random and kept in isolation in plastic boxes (10 cm x 20 cm x 30 cm) with 3-4 cm of decayed leaves and hammock soil. Snails were fed with lichen-covered branches supplemented with a mixture of cornstarch, oatmeal, spinach, vitamins, and calcium carbonate. Snails were maintained at approximately 25ºC, and were sprayed with water 5 times per week until eggs were deposited (24 Sept - 5 Oct). During egg deposition, the egg-producing individuals were marked. After eggs had been deposited, cages were sprayed with water at approximately two week intervals until hatching occurred (Jan - Feb 1987). Parental snails and offspring were then examined for variation at the glucose-phosphate isomerase locus as described above.

FIELD STUDY

The study site was located near Pinecrest, Big Cypress National Preserve, Monroe County, Florida. Pinecrest hammocks (PC) 16 and 16a (numbering system follows Pilsbry, 1946) were separated by a narrow channel of water until the 1960's or 1970's (Hillis *et al.*, 1987; Fig. 1). Prior to connection of these hammocks, *Liguus fasciatus* in PC 16 were of the *walkeri* phenotype (banded shells with pink tips), whereas *L. fasciatus* in PC 16a were of the *barbouri* phenotype (dark snails with white tips); a third phenotype, *aurantius* (orange snails), was uncommon in both hammocks (Hillis *et al.*, 1987). Fire prevention in the Pinecrest area over the past several decades has resulted in increased woody growth around many hammocks, and by the 1960's or early 1970's tree growth (primary willows) had joined the two hammocks sufficiently for movement of *Liguus* between PC 16 and PC 16a (Fig. 1A). Because the two populations are also strongly differentiated at the glucose-phosphate isomerase locus, this site provided an opportunity to study the effects of self-fertilization on the interaction of differentiated populations of *L. fasciastus.*

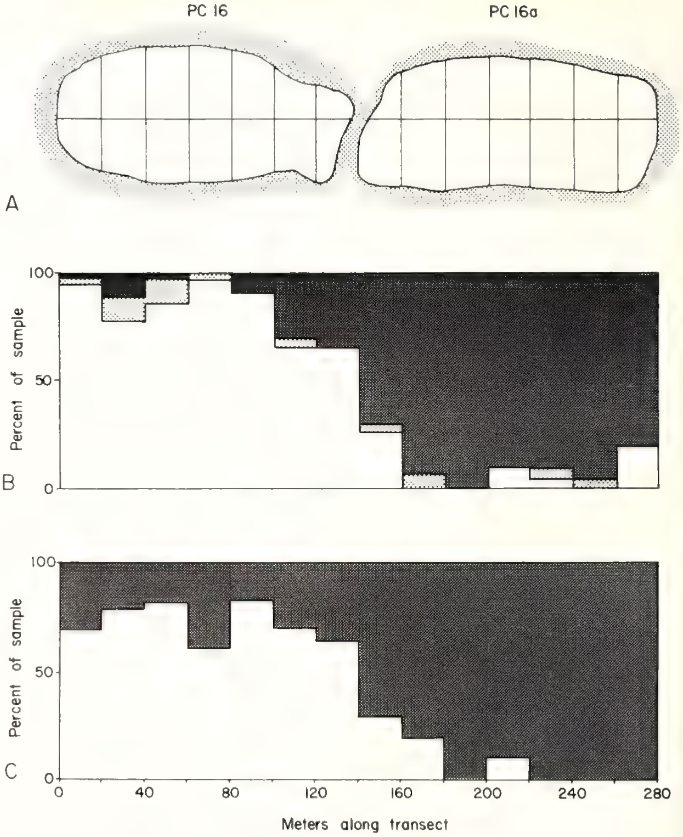

Fig. 1. A. Map of Pinecrest hammocks 16 and 16a, showing location of transect. The shading around the hammocks represents the approximate extent of recent woody growth that is seasonally flooded. This growth provides a connection between the hammocks for movement of *Liguus fasciatus.* **B.** Shell phenotypes of *L. fasciatus* collected in corresponding sections of the transect shown in A. The darkly shaded portion of the histogram represents the percentage of the *barbouri* phenotype, the lightly shaded portion the *aurantius* phenotype, and the white portion the *walkeri* phenotype. **C.** GPI allelic frequencies of *L. fasciatus* collected in corresponding sections of the transect shown in A. The darkly shaded portion of the histogram represents the percentage of the F allele in the sample, and the white portion the percentage of the S allele.

A transect was constructed perpendicular to the axis of the contact through the two hammocks (Fig. 1). Fourteen

20 m intervals were marked along the transect, and snails were collected from sections perpendicular to these 20 m intervals. Between 20 and 44 snails were collected from each section. For each snail, section number and morphological phenotype were recorded; snails were then transferred to the laboratory where each was assessed for genotype at the GPI locus.

ANALYSIS

F-statistics were calculated using the formulae of Weir and Cockerham (1984), which do not make assumptions concerning numbers of populations, sample sizes, or heterozygote frequencies. Indirect estimates of self-fertilization were calculated using the method described by Hedrick (1983). Statistical tests for goodness-of-fit and correlation were conducted as described by Sokal and Rohlf (1981).

RESULTS

Of the 30 pairs of *Liguus* used in the captive breeding experiments, 11 pairs produced clutches of eggs. In one of these pairs, both individuals produced clutches. However, it was determined after the pairings had been made that many pairs came from populations that were fixed for one or the other of the GPI alleles, so only one of the crosses was informative about self-fertilization (Table 1). In this cross, a snail heterozygous for the two GPI alleles (FS) was mated with a snail homozygous for the fast GPI allele (FF). The FS individual produced eggs, and the offspring expressed FF, FS, and SS genotypes (Table 1).

In the field study, both GPI allelic frequencies and shell phenotypic frequencies changed markedly along the transect between PC 16 and PC 16a. The F allele of GPI increased and the S allele decreased along this transect (from PC 16 to PC 16a), and there was a corresponding shift in frequencies from mostly *walkeri* phenotype to mostly *barbouri* phenotype (Fig. 1 and Table 2). Frequencies of heterozygotes at GPI were considerably below Hardy-Weinberg expectations (Table 3).

DISCUSSION

Both population substructuring and self-fertilization appear to have major effects on reduction of heterozygosity in populations of *Liguus fasciatus*. Even though the transect was divided into subpopulations just 20 m wide, variation among subpopulations is very high ($F_{ST} = 0.479$). This value is even higher than the average fixation index for self-fertilizing plants ($F_{ST} = 0.437$; Hamrick, 1983). In addition, the inbreeding coefficient is also very high ($F_{IS} = 0.478$), indicating substantial self-fertilization. The reduction in individual heterozygosity in the study population due to both of these factors (substructuring and inbreeding) is quite substantial ($F_{IT} = 0.728$).

Table 1. GPI genotypes of offspring resulting from 12 crosses of *Liguus fasciatus*.

Number clutches	Maternal genotype	Paternal genotype	Offspring FF	FS	SS
5	FF	FF	76	0	0
6	SS	SS	0	0	106
1	FS	FF	7	6	1

Table 2. Observed GPI genotypes of *Liguus fasciatus* from sections along a transect through Pinecrest hammocks 16 and 16a, and estimates of frequency of self-fertilization (S) in each section.

Section	GPI genotype SS	SF	FF	*S*
1-20 m	24	9	11	.71
21-40 m	29	8	5	.58
41-60 m	26	8	3	.46
61-80 m	17	4	10	.84
81-100 m	25	4	4	.75
101-120 m	20	7	6	.65
121-140 m	10	11	12	.50
141-160 m	5	3	18	.82
161-180 m	5	1	20	.94
181-200 m	0	0	20	—
201-220 m	1	2	17	.62
221-240 m	0	0	20	—
241-260 m	0	0	20	—
261-280 m	0	0	20	—

Except for potential sperm-storage from the previous breeding season, a possibility unsupported by data, the captive breeding data demonstrate that self-fertilization does occur in *Liguus fasciatus*, because only through self-fertilization could the SS offspring result from a mating of FS x FF individuals (Table 1). However, a direct estimation of self-fertilization frequency is not possible from the captive breeding data because of the paucity of appropriate crosses. On the other hand, it is possible to estimate self-fertilization frequency from the transect study.

The proportion of progeny produced by self-fertilization (*S*) can be estimated from the proportion of heterozygous individuals (*H*) in each of the suppopulations in the transect by solving the equation

$$H = \frac{4pq\,(1-S)}{2-S}$$

where *p* and *q* are the allelic frequencies (Hedrick, 1983). This requires the assumption that the subpopulation divisions are small enough to account for population substructuring. Given that individual seasonal movements of *Liguus fasciatus* are typically greater than the 20 m widths of the transect sections (Brown, 1978), this assumption is probably valid. The above calculations were made for each of the subpopulations in which allozymic variation was observed (Table 2). These estimates range from 46% to 94% self-fertilization ($\bar{S} = 0.69$, SD = 0.154). If population substructuring is not fully accounted for by the 20 m transect divisions, then these estimates of self-fertilization are somewhat inflated. An alternative to self-fertilization that could explain the deficiency of heterozygotes is assortative mating. However, in polymorphic populations of *L. fasciatus* mating appears to be random with

Table 3. Expected genotypic frequencies of no self-fertilizing and 69% self-fertilizing models for sections of the PC 16-16a transect, and probabilities of the observed data fitting the expected frequencies. "n.s." designates expected frequencies that do not differ significantly (p > 0.05) from the observed values.

	No self-fertilization				69% self-fertilization			
Section	SS	SF	FF	p	SS	SF	FF	p
1	18.5	20.1	5.5	<.001	23.9	9.5	10.7	n.s.
2	26.0	14.1	1.9	<.01	29.6	6.8	5.6	n.s.
3	24.3	11.3	1.3	n.s.	27.3	5.3	4.3	n.s.
4	11.7	14.7	4.6	<.001	15.5	6.9	8.6	n.s.
5	22.1	9.8	1.1	<.005	24.6	4.7	3.7	n.s.
6	16.7	13.5	2.7	<.01	20.3	6.4	6.3	n.s.
7	7.2	16.4	9.3	<.05	11.6	7.8	13.6	n.s.
8	1.6	9.8	14.6	<.01	4.2	4.6	17.2	n.s.
9	1.2	8.7	16.1	<.001	3.4	4.1	18.4	<.05
10	0	0	20.0	n.s.	0	0	20.0	n.s.
11	0.2	3.7	16.1	<.01	1.2	1.8	17.0	n.s.
12	0	0	20.0	n.s.	0	0	20.0	n.s.
13	0	0	20.0	n.s.	0	0	20.0	n.s.
14	0	0	20.0	n.s.	0	0	20.0	n.s.

respect to shell phenotype (Brown, 1978).

The expected genotypic frequencies under assumptions of no self-fertilization and 69% self-fertilization (the mean of estimates from all subpopulations) are shown in Table 3 and graphically in figure 2. The observed frequencies were tested against the expected frequencies under these two models using a *G*-test (Sokal and Rohlf, 1981). All but one of the genetically variable subpopulations differ significantly from the expected genotypic frequencies under the assumption of no self-fertilization, whereas only one of the subpopulations differ significantly from the expected genotypic frequencies under the assumption of 69% self-fertilization (Table 3). The single subpopulation that differed from 69% self-fertilization expectations differed in having even fewer heterozygous individuals than expected. Given the number of comparisons (10 variable subpopulations), a single departure from expectations at p = 0.05 would be expected by chance 50% of the time, even if the model is correct. Therefore, the transect data are in close agreement with a self-fertilization frequency of approximately 69%.

The frequencies of GPI alleles are strongly correlated with shell phenotypes (Fig. 3), an observation that is probably a result of historical restriction of the *barbouri* phenotype and the F allele to PC 16a, and the *walkeri* phenotype and S allele to PC 16. These two correlations are nearly equally strong and significant: *barbouri*-F allele, r = 0.95, p < .001; *walkeri*-S allele, r = 0.94, p < .001. The third (uncommon) phenotype, *aurantius,* is not significantly correlated with either GPI allele, which is consistent with the distribution of this phenotype in both PC 16 and PC 16a before the contact of the two hammocks. However, the distribution of the two primary phenotypes is asymmetric with respect to the GPI allelic frequencies: the frequencies of *walkeri* are mostly higher than the corresponding S frequencies, whereas the frequencies of *barbouri* are generally lower than the corresponding F frequencies (Fig. 3). This discrepancy may indicate genetic dominance of the *walkeri* genotype over the *barbouri* genotype.

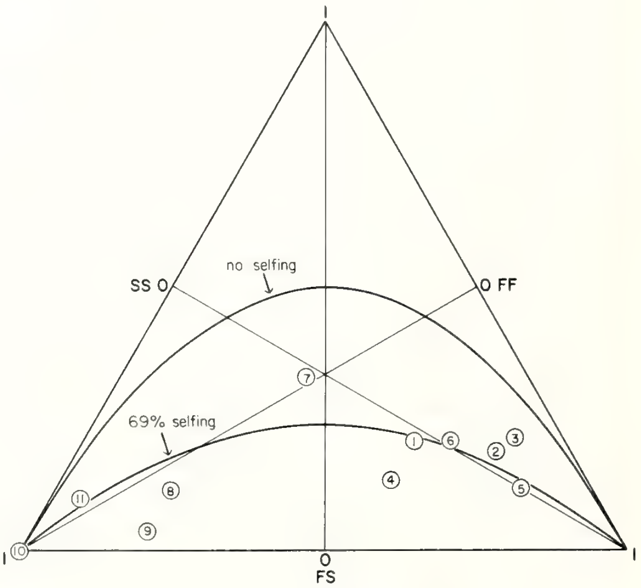

Fig. 2. Trivariate plot of the three GPI genotypes of *Liguus fasciatus* in sections along a transect through Pinecrest hammocks 16 and 16a. The upper curve represents the expected values of Hardy-Weinberg equilibrium without self-fertilization, and the lower curve represents the expected values with 69% self-fertilization. The numbered circles indicate the genotypic combinations of the sections of the transect. The location of section 10 (fixation of the FF genotype) is also the location of sections 12-14.

Roth and Bogan (1984) devised a system for describing phenotypic variation in *Liguus fasciatus* that incorporated twelve distinct characters, each with two to four states. They stated that they chose characters "...in which the alternate states can be seen to segregate in randomly selected material" (Roth and Bogan, 1984). Under the Roth and Bogan system, the three phenotypes present in PC 16 and PC 16a

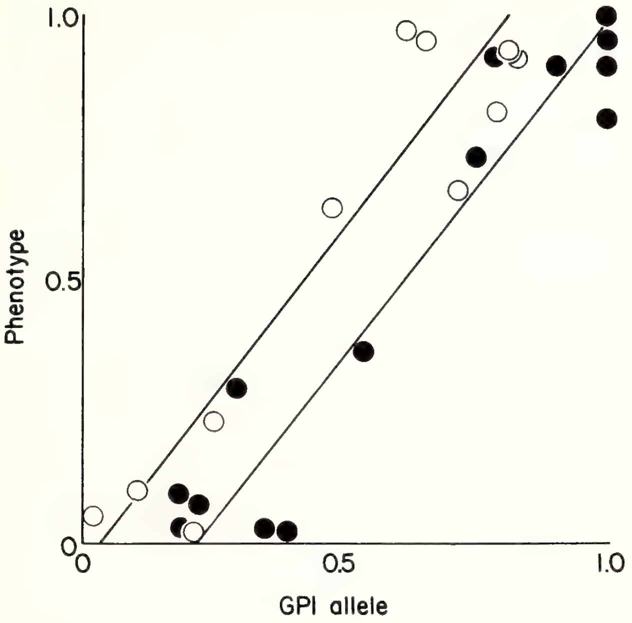

Fig. 3. Correlation of shell phenotypes and GPI alleles through Pinecrest hammocks 16 and 16a. The open circles represent frequencies of the *walkeri* phenotype and the S allele, and the closed circles represent frequencies of the *barbouri* phenotype and the F allele.

are designated as follows: *aurantius:* $C^{Y}B^{Y}S^{+}E^{Y}U^{-}M^{-}L^{O}P^{O}A^{-}O^{-}W^{-}G^{+}$; *barbouri:* $C^{Y}B^{BY}S^{+}E^{B}U^{-}M^{+}L^{B}P^{B}A^{-}O^{-}W^{+}G^{+}$; and *walkeri:* $C^{W}B^{BY}S^{-}E^{B}U^{-}M^{+}L^{B}P^{B}A^{+}O^{+}W^{+}G^{+}$. As only these three phenotypic combinations were observed among over 1,000 examined shells, the independence of the 12 characters seems highly doubtful. If the 12 characters were independent, one would expect 1024 phenotypic combinations of *L. fasciatus* in PC 16-16a, rather than the observed three combinations. Instead, these phenotypes seem to be inherited as single genes. This does not preclude the possibility of a few tightly linked loci, however. Some of the 1021 unobserved phenotypes do occur in other areas (Roth and Bogan, 1984), but probably represent distinct alleles rather than recombinations of the alleles present in PC 16-16a. Obviously, future attempts at understanding the genetics of *L. fasciatus* shell phenotypes must take into account self-fertilization.

Although partial self-fertilization of *Liguus fasciatus* is sufficient to account for the high among-population variation and low within-population variation observed throughout the range of this species, this phenomenon does not account for the overall low allozymic variability (Hillis *et al.*, 1987) compared to the high morphological variability (Pilsbry, 1912, 1946) found in Floridian *Liguus.* The low allozymic variaton could be a result of a relatively recent invasion of few individuals from Cuba, thus giving rise to fixation at most allozyme loci through the founder effect. Fixation at most allozyme loci has occurred in several introduced mollusks that are capable of self-fertilization (Selander and Kaufmanm, 1973; McKracken and Selander, 1980; Hillis and Patton, 1982). However, this does not account for the high morphological variation seen in Floridian populations of *L. fasciatus*. One possibility is that the shell phenotypes are adapted to different local conditions. However, adaptation is unnecessary to explain the distribution and variation of shell phenotypes. Instead, it is likely that the genes responsible for shell phenotype undergo much higher rates of mutation than do the allozyme loci, in which case the partial self-fertilization of *L. fasciatus* would explain the fixation of many of these phenotypes in the numerous isolated Floridian populations of this species.

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MECHANICAL WEAR OF RADULAR DENTICLE CAPS OF *ACANTHOPLEURA GRANULATA* (GMELIN, 1791) (POLYPLACOPHORA: CHITONIDAE)

ROBERT C. BULLOCK
DEPARTMENT OF ZOOLOGY
UNIVERSITY OF RHODE ISLAND
KINGSTON, RHODE ISLAND 02881, U. S. A.

ABSTRACT

Mechanical wear of radular denticle caps of *Acanthopleura granulata* (Gmelin) was examined using light and scanning electron microscopy. Between 6 and 11 transverse rows of teeth are involved in feeding. Wear is first evident as slight abrasion and chipping in rows 8 to 11. Increased wear, chipping, and occasional breakage of the cap subsequently occur. The conspicuous distal black tab on the anterior surface, which is contiguous with the magnetite material of the posterior surface, begins to wear quickly and usually disappears by row 6. The brown and yellow lepidocrocite region, in which the tab is embedded, is mostly worn away by row 4, leaving only an amber base of apatite material with an anterior surface of magnetite. The wearing cap is self-sharpening due to the differential hardness of the leading surface of magnetite and the softer materials of the anterior surface. Presence in the magnetite layer of fibers oriented at about 90° to the posterior surface also contributes to the self-sharpening aspect. The fibers appeared to stop short of the posterior surface; a 90° ventral turn near this surface was not observed. Progressive mechanical wear produces a chisel-shaped tooth that provides an effective grazing capability and indicates a multi-tool feeding strategy.

Although functional morphology of the gastropod radula has been the subject of several studies, little attention has been paid to functional aspects of the highly complex polyplacophoran radula. The relatively few studies of chiton radulae have indicated that as the teeth are used they become worn and are replaced. The process of mechanical wear of the radula has not been described.

The polyplacophoran radula is a ribbon of teeth that can reach a length more than half the length of the animal. Chitons typically have 17 teeth per transverse row and many rows of teeth exist (Fig. 1). Due to substratum contact, the anterior-most teeth are subjected to great stress; Hickman (1980) summarized these forces in her notable précis of gastropod radula functional morphology. The two major lateral teeth per row, also called the dominant teeth because of their functional and visual prominence, are responsible for substratum removal (Fretter and Graham, 1962; Steneck and Watling, 1982; Bullock, 1986). In addition to its use in grazing food particles, the radula appears responsible for creation of the protective homing scars of *Acanthopleura gemmata* (Blainville, 1825) [Chelazzi and Focardi (1983); Chelazzi *et al.* (1983)], *Ceratozona angusta* Thiele, 1909 (Schmidt-Effing, 1980), and *Sypharochiton pelliserpentis* (Quoy and Gaimard, 1835) (Boyle, 1970).

The formative end of the radula is located posteriorly, and increasingly mature teeth are apparent anteriorly. As the teeth at the anterior end of the radula become worn, they are sloughed off and the radular ribbon advances to move fully mature teeth into the feeding position.

Each major lateral tooth possesses a distinct cusp heavily mineralized with the iron compound magnetite. The first study of the mineralization process was published by Towe and Lowenstam (1967), and other recent papers on the subject have appeared. Kim *et al.* (1986a) studied *Clavarizona hirtosa* (Blainville, 1825) and noted four developmental stages of the radular ribbon: stage I, immature teeth composed of a white organic matrix; stage II, with reddish brown denticle caps; stage III, black magnetite becomes evident; and stage IV, fully mineralized denticle caps. While this continuum encompasses the intriguing mineralization process, a complete characterization of radular form must include a functionally critical fifth stage; the anterior-most teeth are being used and becoming worn and lost due to the feeding process.

The structure and general composition of the polyplacophoran radular denticle cap has been the subject of various studies. The posterior surface, which in the feeding

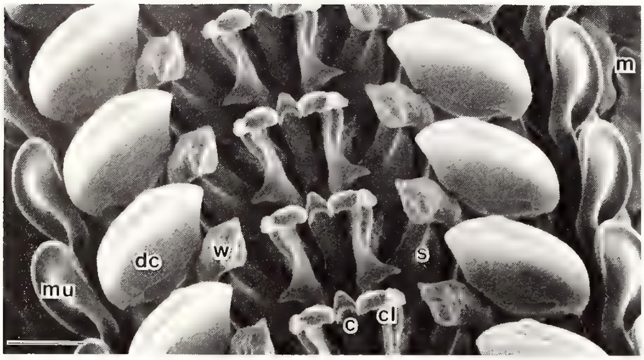


Fig. 1. Scanning electron micrograph of a portion of the radular ribbon of *Acanthopleura granulata*: dorsal view, anterior end toward top of page; specimen from Las Tejitas, Isla de Margarita, Venezuela; c, central tooth; cl, centro-lateral tooth; dc, denticle cap of major lateral tooth; m, marginal teeth; mu, major uncinus; s, shaft of major lateral tooth; w, wing of major lateral tooth (which is broken off as soon as the major lateral tooth is moved into the feeding position); bar = 100 μm.

position is the scraping surface, is covered totally by a substantial shield of magnetite. Colorful microarchitectural units on the anterior surface provide species-specific differences (Fig. 2). A marginal border of black magnetite surrounds areas of brown and yellow lepidocrocite; ventral to the lepidocrocite region is a more transparent, amber portion composed of an apatite mineral (Lowenstam, 1967). A conspicuous black tab of magnetite occurs distally in the lepidocrocite area (Figs. 2A, 16) in most chitonid species.

Several authors have noted that the denticle caps become worn and broken with use (Towe and Lowenstam, 1967; Mizota and Maeda, 1985; Lowenstam and Weiner, 1985; Kim *et al.*, 1986a, b; van der Wal *et al.*, 1987), yet a description of this mechanical wear is lacking. I present information in this paper about mechanical wear of the denticle cap of the major lateral tooth of one species, *Acanthopleura granulata* (Gmelin, 1791), that occurs abundantly from the Florida Keys to the West Indies. Evidence from gastropod studies provides valuable insight into the interpretation of the limited information now available on the chiton radula.

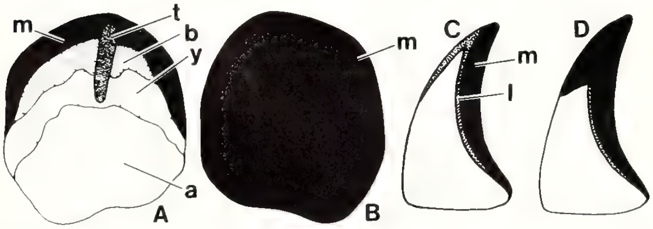


Fig. 2. Distribution of microarchitectural units of the *Acanthopleura granulata* denticle cap [adapted from Lowenstam (1967)]: **A,** anterior view; **B,** posterior view; **C,** longitudinal section near tab; **D.** longitudinal section through tab [a, amber component (apatite); b, brown component (lepidocrocite); l, lepidocrocite; m, magnetite component (black); t, tab (magnetite); y, yellow component (lepidocrocite)].

MATERIALS AND METHODS

Radulae of *Acanthopleura granulata* were examined utilizing light and scanning electron microscopy (SEM). Specimens were collected at northeastern Key Largo, Florida (1986, n=13), Indian Key Fill, Florida (1977, n=44), Las Tejitas, Isla de Margarita, Venezuela (C. Franz, leg. 1987, n=12), and Playa Picua, La Blanquilla, Venezuela (C. Franz, leg. 1986, n=8). Radulae were extracted from the animals, cleaned in a heated 2N KOH solution, and placed in a series of distilled water rinses in an ultrasonic cleaner. Some specimens were kept in 70% ethanol and studied using a Wild M•8 stereozoom dissecting microscope with a 1.6X adapter. Fully mineralized denticle caps often cracked longitudinally when air dried; however, the denticle caps of a few radulae were broken with microforceps to create additional fracture surfaces. The radulae used for SEM were teased into pieces and mounted on aluminum specimen mounts with Scotch Double-Coated Tape No. 666. The specimens were coated with carbon and then 60% gold:40% palladium in a Denton DV-502 vacuum evaporator with a rotating/tilt device. All SEM work was done on an ISI MSM-3 located in the Department of Zoology, University of Rhode Island.

Characterization of tooth wear began by numbering the transverse tooth rows beginning at the anterior end of the radular ribbon. To measure denticle cap height, the anteriormost 15 transverse rows of teeth were isolated and the individual major lateral teeth of one side were teased apart and transferred to a double-coated tape surface or modeling clay where they were positioned using an insect pin. Height measurements were made using the Wild M•8 with a drawing tube and stage micrometer. The height of unused denticle caps was determined, and all worn caps were recorded as a percent of this value.

Living *Acanthopleura granulata* from Crawl Key, Florida (1987, n=7) were maintained in an aquarium. The feeding process was observed and photographed using video equipment.

It was evident that two potential directional problems exist. First, investigators of the mineralization process understandably number the transverse tooth rows beginning at the posterior formative end, although there is some disagreement about where to begin numbering. However, because tooth developmental processes are not always synchronous among individuals (Lowenstam and Weiner, 1985), and because an investigation of tooth wear involves only a limited number of transverse tooth rows in the feeding position at the anterior end of the radular ribbon, it appeared crucial for mechanical wear studies that the numbering begin with the most worn row at the anterior end of the ribbon and proceed posteriorly. Only this procedure allowed an adequate comparison among individuals.

A second directional problem could arise regarding the surfaces of the denticle cap. The solid magnetite scraping surface of the denticle cap faces posteriorly in the formative and fully mature stages. Authors are consistent in calling this surface the posterior surface. However, in an incorrect application of a generalized gastropod model to the function of the chiton radula, the radula is protruded from the mouth and the posterior surfaces of the teeth, which are now pointing anteriorly, are moved anteriorly and then dorsally, bringing grazed particles into the buccal cavity. It would be tempting to stress the functional process and to designate the scraping surface as the anterior surface. Although this generalized model might be seen in some chiton groups, literature reports indicate that, at least in the Suborder Chitonina, the opposing major lateral teeth, that spread apart as the chiton begins to feed, converge medially, forming characteristic grazing marks that are perpendicular, not parallel, to the longitudinal axis of the animal (Jüch and Boekschoten, 1980; Bullock, 1986). It seems best to retain the current terminology and accept the fact that the chiton produces and manipulates the radular ribbon in a way that greatly changes these directions during the feeding process.

RESULTS

Mechanical wear of the denticle caps of the major lateral teeth was evident in all individuals examined. This wear was seen as abrasion, slight chipping, and, occasionally, breakage. Observation of *Acanthopleura granulata* feeding on the sides of glass-walled aquaria indicates that in each feeding event about 7 to 10 pairs of denticle caps typically sweep the substratum. It is unclear exactly how many of these teeth actually make contact with the substratum, but studies utilizing Plexiglas indicate that each feeding event results in 3 to 6 pairs of grazing marks. Irregular substrata could provide quite different results. Abrasion and reduction of denticle cap height begin soon after the teeth move anteriorly enough to be involved in the feeding process (Fig. 3). Use of the teeth causes sporadic chipping of the distal end of the denticle caps, and plots of denticle cap height are irregular because of this phenomenon. Denticle cap height declines with use until the major lateral tooth is discarded. Occasional denticle caps are broken off near their base.

The distribution of the different components of the denticle cap was evident by the color pattern on the anterior surface. The colors of the non-magnetite units were not the same as Lowenstam (1967) reported for *Acanthopleura echinata*. The lepidocrocite in *A. granulata* was seen as a distal brown band and a more ventral yellow layer (Fig. 2A). Lowenstam (1967) noted that the colors of this unit differ due to transparency and their proximity to other components.

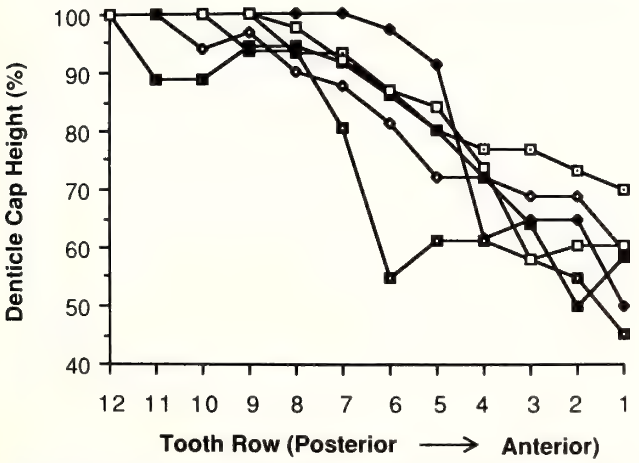
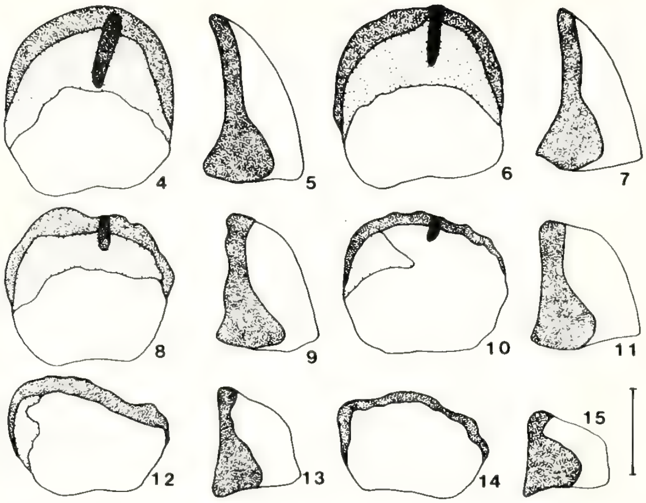


Fig. 3. Denticle cap height vs. transverse tooth row at anterior end of radular ribbon; Las Tejitas, Isla de Margarita, Venezuela, n = 6.

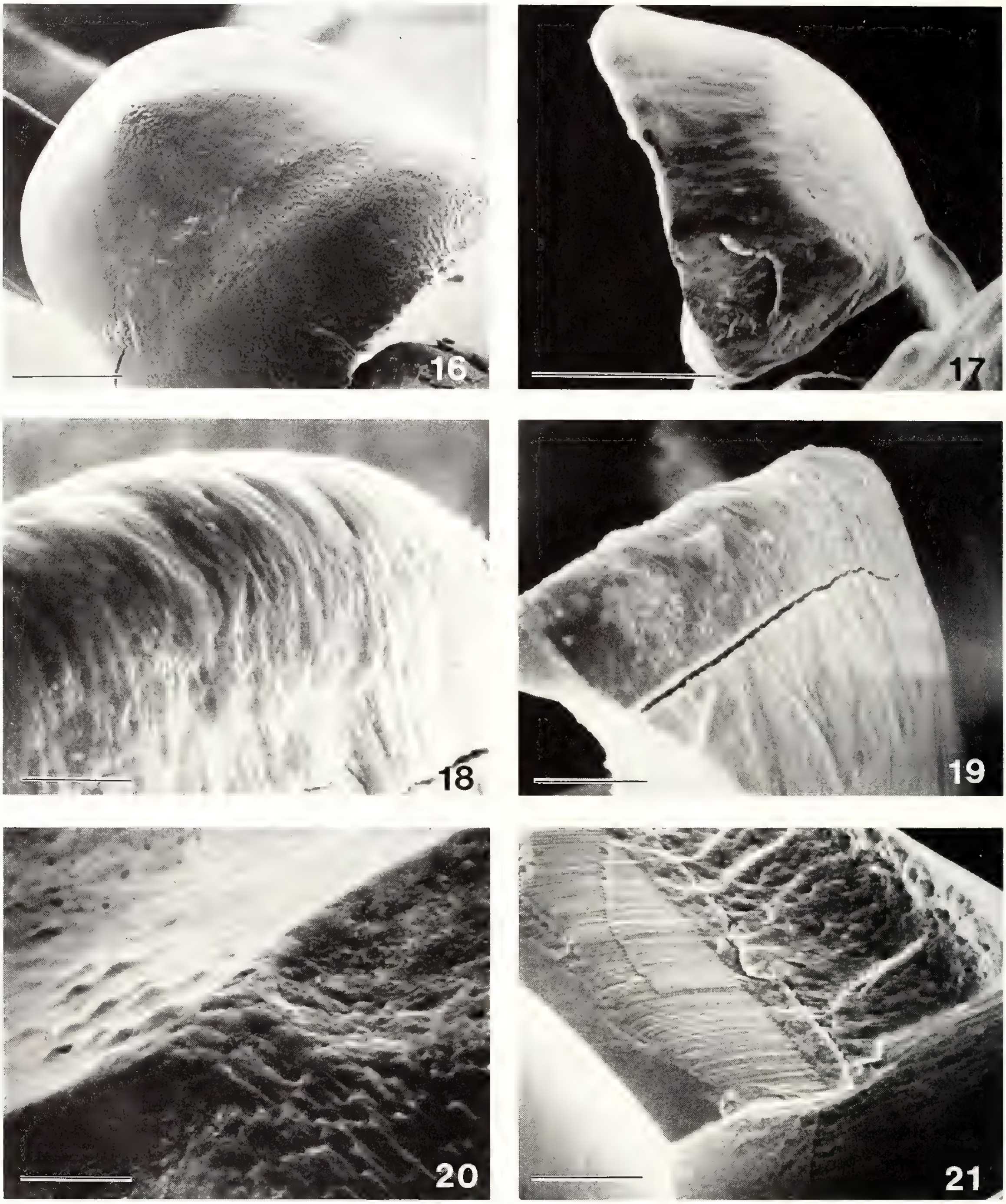


Figs. 4-15. Outline drawings of denticle caps showing mechanical wear, anterior and lateral views (single individual, NE Key Largo, Florida). **Figs. 4, 5.** Transverse tooth row 14 (unused), with all exterior components fully visible. **Figs. 6, 7.** Row 11, slight chipping of distal edge evident. **Figs. 8, 9.** Row 6, increased chipping, decreased height, reduction of distal tab, magnetite, and lepidocrocite units. **Figs. 10, 11.** Row 5, tab nearly gone (typically lost by this time), lepidocrocite worn away except at lateral margin. **Figs. 12, 13.** Row 3, tab absent, mostly amber base with magnetite scraping surface. **Figs. 14, 15.** Row 1, lepidocrocite absent. Anterior views do not differentiate the brown and yellow bands of lepidocrocite; lateral view only shows magnetite unit; bar = 200 μm.

The denticle caps of *Acanthopleura* fixed and preserved in 70% ethanol tended to separate quite easily from the shaft of the major lateral tooth, especially after a few years in alcohol. This situation was not seen in freshly preserved animals, and it is obvious that in living *Acanthopleura* the denticle cap is very securely attached to the shaft.

Light and scanning electron microscopy of denticle caps allowed a clear view of mechanical wear as well as information about microstructure. Fully mineralized caps often fractured when air dried, and the resulting cracks afforded various sectional views of cap morphology. The microarchitectural units were easily seen with light microscopy because of their color differences (Figs. 4-15). Tooth rows 8 to 11 showed slight abrasion and chipping of the black magnetite of the distal end. By row 5, the black tab had disappeared totally in most cases. Loss of most of the lepidocrocite layer was evident by rows 4 to 5 (Fig. 10). The denticle caps in rows 1 to 4 were quite stubby and only the amber apatite base and the black magnetite layer of the posterior (cutting) surface were present (Figs. 12-15).

Abrasion of the anterior surface was readily apparent with scanning electron microscopy (Figs. 16-21). The wearing teeth remained chisel-shaped. Examination of fracture sur-



Figs. 16-21. Scanning electron micrographs of *Acanthopleura granulata* denticle caps. **Fig. 16.** Unused denticle cap showing rounded distal end and granular tab; Indian Key Fill, Florida; bar = 100 μm. **Fig. 17.** Lateral view of denticle cap from first (most worn) transverse row; note abrasion on sides and anterior surface; Las Tejitas, Isla de Margarita, Venezuela; bar = 100 μm. **Figs. 18, 19.** Distal lip of worn caps showing abrasion and self-sharpening due to orientation of fibers in magnetite unit. **Fig. 18.** Tooth row 2, bar = 10 μm. **Fig. 19.** Tooth row 4, bar = 20 μm; Las Tejitas, Isla de Margarita, Venezuela. **Fig. 20.** Cross section through distal portion of denticle cap showing granular tab of anterior surface (upper left) and the magnetite fibers that extend from tab toward posterior surface (lower right); NE Key Largo, Florida; bar = 10 μm. **Fig. 21.** Fractured distal portion of denticle cap revealing fibrous microstructure of posterior surface; note smooth margin at posterior surface (lower left); NE Key Largo, Florida; bar = 20 μm.

faces revealed the fibrous construction of the magnetite layer (Fig. 21). These fibers, that at times appear as lamellar clusters, are oriented at about 90° to the posterior surface of the denticle cap. I was unable to verify that the fibers bend ventrally at or near the posterior surface; a smooth margin was observed in this region (Fig. 21).

Mechanical wear of the radula apparently proceeds at different rates in different geographic locations. Wear quickly reduces denticle cap height past the black tab in some populations, but in other localities the tab is visible through more tooth rows. In severe cases, the first 4 or 5 tooth rows are missing all of the tab and all lepidocrocite. Even in a single population, there is considerable wear difference between individuals.

DISCUSSION

The presence of iron compounds in the denticle cap material of limpets and chitons has intrigued biologists and geologists for decades. The hardened nature of the radula has important implications for those interested in the biological precipitation of these iron compounds and the behavioral and ecological consequences of this hardness. Pioneering work in the area of limpet radular structure was done by Jones *et al.* (1935) and Runham and his co-workers (Runham and Thornton, 1967; Runham *et al.*, 1969). A few investigators have reported on the radula of the Polyplacophora (Tomlinson, 1959; Runham, 1963; Carefoot, 1965; Lowenstam, 1967; van der Wal *et al.*, 1987), and recently some workers have focused their efforts on the biomineralization process (Towe and Lowenstam, 1967; Lowenstam and Weiner, 1985; Mizota and Maeda, 1985; Kim *et al.*, 1986a, b). These studies have shown that the cusps of limpets and chitons are a composite of different materials and that the specific materials present and their distribution have important functional aspects.

Lowenstam (1967) presented diagrams of the posterior, anterior, and longitudinal cross section of the denticle cap of *Acanthopleura echinata* (Barnes, 1824). I accept these diagrams as factually correct with the exception of the longitudinal cross section (similar to my Fig. 2C) which fails to show the existence of the conspicuous black tab of the distal anterior surface. Many of the longitudinal fractures that occur during drying fail to develop at the site of the black tab. However, I observed fracture surfaces in the region of the tab, and I was able to see that the magnetite at this site is broad at the surface but it narrows before joining the magnetite of the posterior surface. Of course, examination of the anterior surface of a denticle cap, including Lowenstam's diagram, would dictate the inclusion of the tab in a longitudinal cross section (Fig. 2D). Lowenstam (1967) stated that due to the intervening lepidocrocite, the magnetite layer does not directly contact the apatite. However, I observed that the tab magnetite penetrates the apatite at its most distal portion (Fig. 20), and I saw no lepidocrocite where this intrusion occurs. The continuity of the magnetite between the tab and the posterior surface provides substantial support for the tab (Fig. 2D).

The magnetite is present in functionally important areas of the *Acanthopleura* and *Chiton* denticle cap. The entire posterior surface, the scraping surface, is completely covered with a substantial layer of magnetite. The anterior surface, which is less subjected to the rigors of substratum contact, has a narrow marginal band of magnetite that is contiguous with that of the posterior surface. Elsewhere across the distal anterior surface, only lepidocrocite is present except for the magnetite of the tab. Bullock (1986) stated that use of magnetite in the denticle cap is conserved. However, it is important to recognize that the denticle caps function very effectively and that any additional magnetite might provide additional hardness but disrupt the self-sharpening phenomenon. For example, more magnetite on the anterior surface would provide protection but would interfere with self sharpening. Presence of the tab provides some of this protection but at the same time allows the softer lepidocrocite and apatite layers to become worn.

I suggested previously (Bullock, 1986) that the tab could protect the otherwise unprotected anterior surface during movement of the radula across the substratum. The tab often begins to disappear quickly when the cusp is used for feeding. At this point, many of the cusps involved in feeding already have worn down past the tab. Any protection provided by the tab during feeding is better than no protection, and the chiton is well served by even a brief existence of the tab. However, the observation that the tab disappears quickly indicates that the tab could also function to protect the anterior surface *prior* to tooth use. The radular ribbon remains inwardly curled until the tooth rows are moved into the feeding position; some aspects of radular morphology reflect passive accommodation of the teeth because of "curled" contact; other morphological features appear to have a pre-feeding functional basis. Lacking protection, the denticle caps could abrade each other during normal movement of the animal over irregular substrata. Within column abrasion of the anterior surface by the posterior surface of magnetite of the next cap is prevented or minimized by: (1) interleaving of the major uncinus (Fig. 1, mu) between denticle caps, and (2) presence of the tab. Contact with the opposing denticle cap is prevented by the wing of each major lateral tooth (Fig. 1, w). The wings are broken off immediately upon movement of the tooth row into the feeding position.

The existence of a fibrous microstructure in the magnetite was not unexpected. Runham and Thornton (1967) and Runham *et al.* (1969) noted 800 Å thick fibers in the mineralized cusps of *Patella vulgata* Linnaeus, and Towe and Lowenstam (1967) had reported a fibrous network in the development of the denticle cap of *Cryptochiton stelleri* (Middendorff, 1847). More recently, van der Wal *et al.* (1987) briefly commented on "closely packed rod-shaped and elongate concavo-convex (trough-shaped) units" in the denticle cap of *Chiton olivaceus* Spengler, 1797. According to the latter authors, within the magnetite unit the fibers are oriented perpendicular to the posterior surface, but they turn ventrally 90° near the posterior surface. Although fibers and lamellar clusters of fibers are easily observed in SEM of fractured *Acanthopleura granulata* denticle caps, I was unable to see clear evidence of their ventral turn in my preparations. I almost always found that the visible fibers stopped short of the posterior edge, which appeared rather smooth in cross section. This smooth boundary could be the region where the fibers are oriented parallel to the posterior surface, but my preparations, and perhaps the limited resolution of the available SEM, did not document any change in fiber orientation.

The existence of fibers within a matrix is a critical feature of the functional morphology of the polyplacophoran denticle cap, but just how these components provide the obvious hardness of the tooth is a question with an exceedingly elusive answer. Vincent (1980: 132) concluded that "the hardness of biological materials has not attracted the attention of experimentalists . . . It is not only a difficult measurement to make but its interpretation can be fiendishly difficult. The hardness of *artificial* composites, whose variables can be closely controlled, is a subject that has hardly yet been broached, let alone the hardness of the much more complex biological composites."

The mineralized cusps of limpets and chitons wear down yet maintain a rather sharp cutting edge (Runham and Thornton, 1967; Runham *et al.*, 1969; Bullock, 1986; van der Wal *et al.*, 1987). This self-sharpening phenomenon is due to the hard but thin leading posterior surface and the relative softness of the much thicker anterior portion of the cusp. Furthermore, the orientation of the fibers assists by fracturing lengthwise, which helps to maintain the wedge angle. The wedge angle of *Acanthopleura granulata* is about 60° in unused teeth, but with wear this angle can increase to as much as 70°. The fibers parallel to the surface along the leading posterior edge, which are well documented in *Patella* and reported in *Chiton olivaceus* (van der Wal *et al.*, 1987), are less susceptible to wear (Runham *et al.*, 1969), and this distal edge is the actual cutting portion of the denticle cap. As denticle caps of *A. granulata* become worn with use, the distal edge is seen as a slightly thickened lip (Figs. 17-19).

The fibers of the tab magnetite that proceed to the posterior surface are oriented to assist, or at least allow, self-sharpening when mechanical wear affects this level; this orientation also means that the fibers at the anterior surface are nearly perpendicular to it, and the exterior portion of the tab has increased resistance to wear. The conspicuous granules of the tab are surface protrusions of the underlying fibers or clusters of fibers of magnetite (Fig. 20).

The form of the unused denticle cap could perhaps not be the most efficient morphology; as Hickman (1980) noted, it could be important functionally for the teeth to wear down to be efficient. A variation of this theme would be the recognition that in the feeding position, the continuum from new to worn teeth would provide different capabilities and that it would be advantageous to graze on heterogeneous substrata with a multi-tool approach. All denticle caps of this continuum, including those of the anterior-most transverse row, suffer mechanical wear, indicating that the major lateral teeth continue to function until they are lost.

No studies of chiton radulae have examined intraspecific differences due to life on substrata of varying hardness. The number of teeth that become substantially worn varied greatly from individual to individual within a single population, and the anterior-most teeth were not worn to the same degree. In some *Acanthopleura granulata* maintained in a glass aquarium for two weeks, most of the denticle caps in the feeding position still retained at least some of the distal anterior tab, indicating that wear had not proceeded at the same rate as that of the teeth from field-collected and fixed individuals.

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BEHAVIOR, BODY PATTERNING, GROWTH AND LIFE HISTORY OF *OCTOPUS BRIAREUS* CULTURED IN THE LABORATORY

ROGER T. HANLON
MARTIN R. WOLTERDING
THE MARINE BIOMEDICAL INSTITUTE
THE UNIVERSITY OF TEXAS MEDICAL BRANCH
GALVESTON, TEXAS 77550-2772, U.S.A.

ABSTRACT

A total of 10 years of laboratory observations are reported, centering mainly upon four groups of *Octopus briareus* Robson cultured through the life cycle. Details are given for rearing methodologies, system design, egg development, hatching and feeding. A detailed analysis of growth indicated that this species grows at a fast exponential rate (4.8% mean increase in body weight per day) for the first 18 - 20 weeks, then growth slows to a logarithmic rate for the remaining 30 weeks of the life span. Growth is allometric, with arms III growing faster and larger than arms I, II and IV to become a chief morphological character of the species. *O. briareus* is susceptible to bacterial skin lesions and this species is strongly cannibalistic. Life span is estimated to be 10 to 17 months.

The emphasis of the study was behavior. The morphology and development of body patterns are described, with detailed descriptions of the 18 chromatic, four textural, nine postural and four locomotor components of patterning. Aspects of exploratory behavior as well as intraspecific (agonistic, reproductive) and interspecific interactions (attack, defense) are described using body patterns as the bases of description.

Octopuses have been the subject of folklore for centuries (Lee, 1875; Aristotle *In:* Peck, 1970; Lane, 1974), but more recent and comprehensive scientific accounts of octopus biology (e.g. Robson, 1929a, b, 1932; Pickford, 1945; Wells, 1978; Boyle, 1983, 1987) have helped clarify our understanding of these active carnivores that have a short life span but occupy a high trophic level in the marine ecosystem. Many gaps remain, especially in our knowledge of how octopuses behave, grow and reproduce in nature. This study was initiated in 1969 to fill in some of those gaps for *Octopus briareus* Robson.

This laboratory study was conducted by Wolterding in Miami from 1969-1971, by Hanlon in Miami from 1972-1975, and later by Hanlon and Forsythe in Galveston from 1980-1984. In all, four groups of *Octopus briareus* were cultured through the life cycle so that the observations herein come from hundreds of animals from different populations and year classes.

LABORATORY CULTURE

MATERIALS, MEASUREMENTS AND WATER QUALITY

In 1969 and 1972, *Octopus briareus* eggs or gravid females were obtained by skin or SCUBA diving in shallow water (1 - 2 m) south of Miami, Florida (Card Sound, Soldier Key, Key Largo) and transferred to the open seawater system at the Rosenstiel School of Marine and Atmospheric Science, University of Miami, on Virginia Key. The system was described in detail by Myrberg (1969). All tanks were subject to indirect sunlight. Therefore the light, temperature, and salinity cycle closely resembled the natural environment throughout the year. Wolterding reared five adults to maturity (one laid fertile eggs) from about one hundred hatchlings in 1969-1971 and made behavioral observations (between 1000 and 1200 hours) on 24 individual octopuses, some of which were field-caught and maintained. Hanlon reared eight adults to maturity from about one hundred hatchlings in 1973 and made growth measurements and behavioral observations.

In 1981 in Galveston, Texas, 34 eggs were obtained from the Dallas aquarium, where a female imported from Florida had laid eggs. Eight octopuses were cultured through the life cycle and produced second generation eggs and hatchlings. In 1982, portions of two broods of eggs (n = 300) were collected from Sweeting's Pond on Eleuthera Island, Bahamas, and shipped to Galveston. Thirty octopuses were cultured through the life cycle and five females produced second generation eggs. A growth analysis and extensive

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observations on body patterning were made on these octopuses. The large closed seawater system in which they were cultured has been described by Hanlon and Forsythe (1985).

Small octopuses were anaesthezied either in 1½% ethyl alcohol/sea water or 1½ - 2½% ethyl carbamate (urethane)/sea water. For adults, the concentrations were raised to 3% of each solution. It usually took one to four minutes to completely relax the octopuses. Urethane relaxes the arms very well and is excellent for growth measurements, but the animals reacted violently to it for the first 30 seconds. Alcohol does not relax the arms very well but the octopuses react calmly to it. Therefore, in later experiments on adults, a combination was used, consisting of either (1) 3% alcohol followed by 1½% urethane, or (2) 3% alcohol mixed with 1½% urethane. The animals did not react violently and the arms relaxed well. It was important to wash the animal off briefly with fresh sea water and to keep it slightly moist while measuring it. Afterwards the octopus was held by hand and a mild jet of sea water sprayed into the mantle over the gills. Usually in one to three minutes the octopus ventilated and regained muscle control and alertness. No mortalities resulted from this procedure.

Growth measurements were taken with dial calipers on live, anaesthetized octopuses throughout the life cycle. The length measurements are illustrated in figure 1. First and third right arm lengths were measured since they represented the shortest and longest arms, respectively. In all cases the relaxed arms were gently stroked outward then measured several seconds later after they were stationary. For wet weights, octopuses were held momentarily with the mantle highest so that excess water drained out, then weighed to the nearest 1.0 mg.

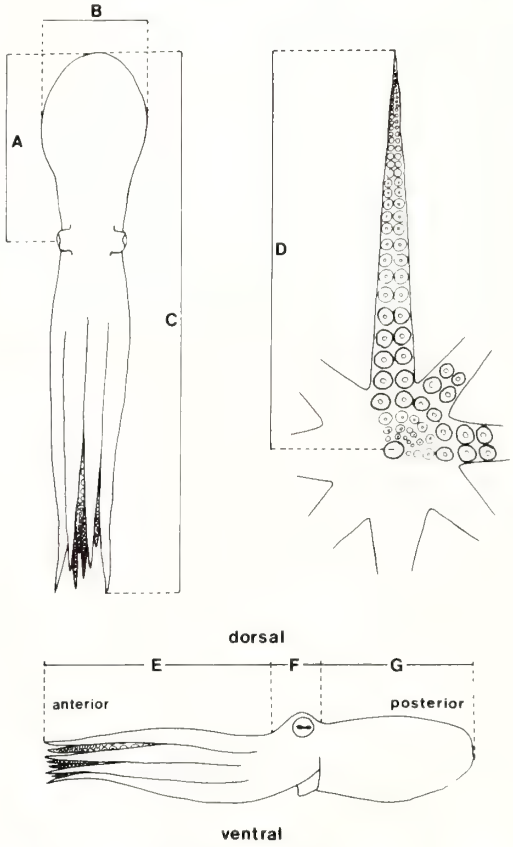


Fig. 1. Growth measurements and terminology. A - mantle length, B - mantle width, C - total length, D - arm length. For behavioral terminology: E - arms, F - head, G - mantle.

Still photography was used extensively in documenting behavior and body patterns. Approximately 930 photographs were taken in the laboratory and 230 in the field. A 35 mm Asahi Pentax or Nikon camera system was used with various close-up lens and bellows units (for magnification up to 16 : 1) and color slide film and electronic flash. Underwater photographs were taken with a Nikon F and 55 mm Micro-Nikkor lens and electronic flash in a Lexan housing.

Water quality in the open system in Miami was monitored only for temperature (mean 25°C, range 18 - 29°C) and salinity (mean 33 ppt, range 27 - 36 ppt). The closed systems in Galveston were monitored for many parameters. Most octopuses were cultured between 20 and 26°C, 32 - 38 ppt salinity and at a pH of 7.8 - 8.2. A pH below 7.5 begins to affect octopus metabolism adversely. Sustained levels of ammonia-nitrogen (NH_4 -N) and nitrite-nitrogen (NO_2 -N) were generally kept below 0.2 mg/*l*, but on rare occasions octopuses tolerated levels as high as 10.4 mg/*l* NH_4 -N and 0.3 mg/*l* NO_2 -N for a few days. Sustained levels of nitrate-nitrogen (NO_3 -N) were generally kept below 200 mg/*l*, but levels as high as 650 mg/*l* for several days produced no observable ill effects. The key to this tolerance of high levels of nitrogenous waste was maintenance of pH between 7.8 and 8.2. These high levels of tolerance are in general agreement with the findings of Hirayama's (1966) short-term experiments on *Octopus vulgaris* Cuvier in Japan. The 2600 *l* closed seawater system in which *O. briareus* was cultured in 1982 was found to support 15 kg of octopus biomass and still maintain nitrogenous levels at an acceptable level (Hanlon and Forsythe, 1985).

REARING METHODS

In 1969 Wolterding reared hatchlings in floating plexiglass boxes (with screened sides) for the first 50 days, in 12 *l* aquaria until day 102 and in 40 *l* glass aquaria thereafter. Plexiglass sheets were affixed over the tops of the aquaria to prevent escapes. For dens, small clear plastic vials or artificial grass were used for the youngest animals, while large rocks, unglazed earthenware and flower pots were provided for large octopuses. Hatchlings were hand-fed disarticulated crab legs for the first two weeks; thereafter they ate small live crabs (*Uca* sp.).

In 1973 Hanlon reared some hatchlings as Wolterding did, while other octopuses were reared solely on live crabs in a broad but shallow (7 cm water depth) water table in which octopuses hiding in the bottom of the floating artificial grass could see and easily attack the crabs crawling just below them. Large numbers of crabs were kept in the tank to concentrate the food source and thus enhance feeding. As the octopuses grew, an excess of small mollusc shells and irregularly shaped rocks were added for shelter. The distance from the water level to the top of the tank sides was 12 cm and thus prevented small octopuses from crawling out. At two months, octopuses were moved to 75 *l* aquaria with flower pots to hide in, and hinged tops were secured to the tanks or screened wooden frames were fit snugly over the top of the tanks. For growth studies individual animals were reared in separate aquaria.

In 1981 and 1983 in Galveston, the same group-rearing concept of Hanlon's 1973 study was used in which shallow water tables were stocked with (1) octopuses (density equivalent to 300 - 700 hatchlings per m^2), (2) numerous small polyvinyl chloride (PVC) sections of pipe for hiding, and (3) high densities of small mysid shrimps (genus *Mysidopsis*). The sizes of pipe and shrimp were increased as the octopuses grew. Due to the cannibalistic nature of *Octopus briareus*, octopuses had to be reared in separate containers after about two months to achieve good survival (Hanlon and Forsythe, 1985). Octopuses up to 1 kg could be grown in containers as small as 28 cm diameter and 21 cm deep with screened sides to allow water exchange. For some growth data, some octopuses were cultured through the entire life cycle in perpetual isolation, beginning with 50 m*l* plastic cups with screened sides for hatchlings; these animals showed no obvious physiological or behavioral deficits.

EGG DEVELOPMENT AND HATCHING

The large eggs measure 10 - 14 mm long and 4 - 5 mm wide, with a stalk 5 - 10 mm long. The stalks of seven to 34 eggs (mean 25) were intertwined onto a central strand 8 - 10 cm long that was attached by the female to the substratum (Fig. 2). Development took 50 - 80 days at 19 - 25ºC, during which time the embryos underwent two reversals (Fig. 3). From two to seven days before hatching the embryo rotated 180 degrees toward the distal end of the egg and a seam developed across the distal third of the egg. Physical stimulation of the egg (by the mother or experimenter) resulted in (1) increased respiration and arm movements, (2) expansion of chromatophores over the embryo, (3) one or two rotations of the embryo and (4) occasional squirting of ink within the egg. This increased movement (and secretions from Hoyle's organ, which releases a lytic enzyme) caused the egg seam to split, and hydrostatic pressure within the egg ejected fluid and part of the mantle out of the egg (Fig. 4). Within seconds or a few minutes the octopuses managed to jet or squeeze their way out of the egg. Hatching occurred generally at night, and hatching success was very high, mainly greater than 95%. Females characteristically laid and actively brooded (Fig. 5) about 200 - 500 eggs, although one laboratory-cultured 500 g female in Galveston laid 955 eggs in 1981. Many eggs in this study were removed from the mother and brooded artificially by suspending them over gently bubbling water. The hatchlings were fully formed, miniature adults that had no planktonic phase; they would often crawl, ink, jet, change color and feed within moments of hatching (Messenger, 1963). They could survive up to ten days on internal yolk. Sometimes the hatchlings had a small external yolk sac (1 - 3 mm); hatchlings seven to ten days premature had a large external yolk sac and did not survive well.

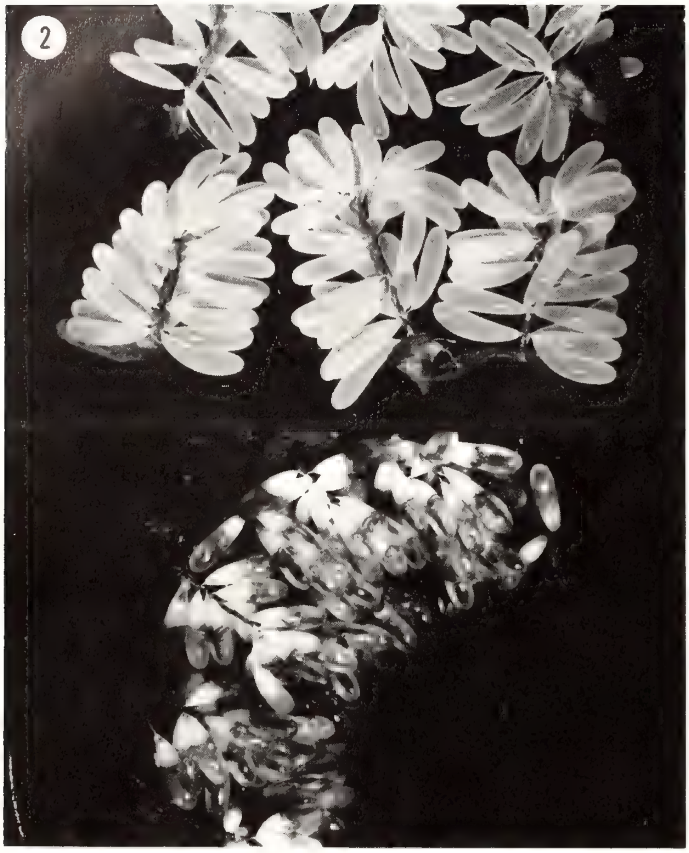
FOODS

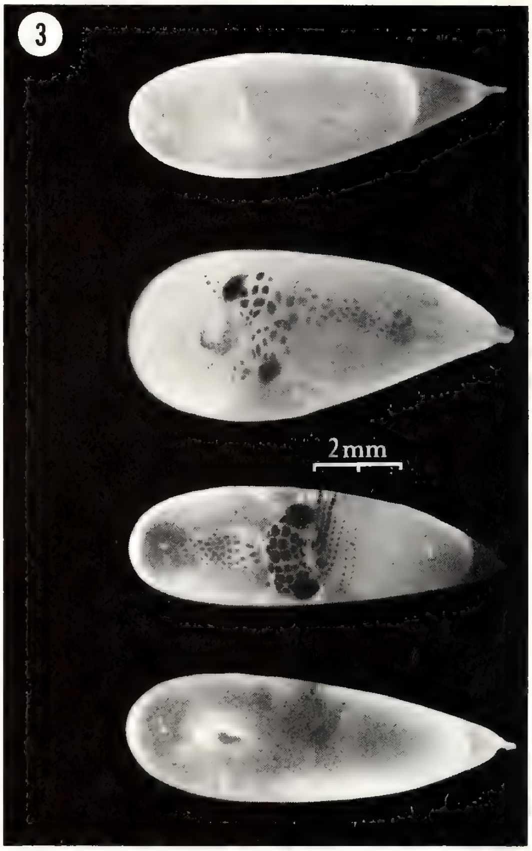
Live crabs are the favorite food of *Octopus briareus* of all sizes, but they will accept a wide range of crustaceans, molluscs, polychaetes and fishes. They will readily attack and capture prey that are from 1/3 to 2X their own mantle length. Table 1 lists species that *O. briareus* will attack and/or eat in the laboratory. Over 500 feedings were observed and a few observations are noteworthy. The gastropods *Fasciolaria tulipa* Linné and *Strombus gigas* Linné were attacked repeatedly but always released within one minute. The stomatopod *Gonodactylus* sp. was eaten despite having stabbed the octopus several times. Crabs were relatively defenseless and appeared paralyzed within three minutes after capture. Hermit crabs were eaten by pressing the apertures of their shells against the buccal mass of the octopus; after five to ten minutes, one arm reached into the shell and extracted the crab. The horseshoe crab, *Limulus polyphemus* Linné, appeared to be too difficult to eat. It took about 30 minutes to see the effect of paralysis from the octopus venom, and the octopus tried unsuccessfully for five and one-half hours to disarticulate and eat the crab.

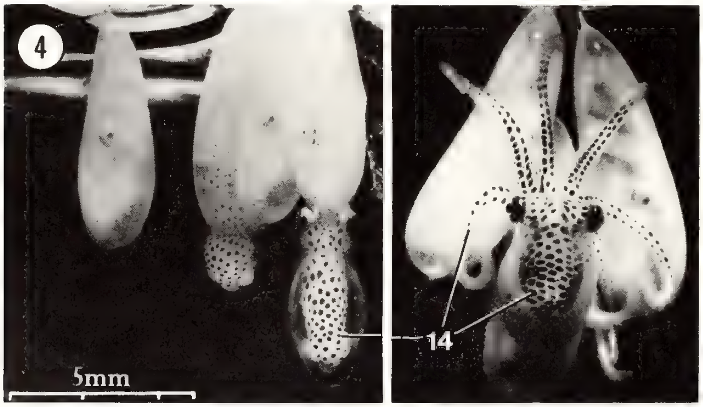
GROWTH RATES BY LENGTH AND WEIGHT

The following growth data are available: five octopuses reared to maturity in an open seawater system in Miami in 1969; eight animals grown to maturity in the same open system in Miami in 1973; eight octopuses reared to maturity in a closed seawater system in Galveston in 1981; and 20 animals weighed and measured from hatching to maturity during a large-scale culture effort in a closed seawater system in Galveston in 1983. In the latter two experiments, numerous broods of second-generation eggs were produced. The growth results in all experiments were remarkably consistent and indicate clearly that *Octopus briareus* increases in length and weight exponentially during the first 16 to 20 weeks of the life cycle, after which growth slows to a more typical logarithmic form until senescence and death. At hatching *O. briareus* is approximately 6 mm mantle length (ML) and 95 mg wet weight (WW). The largest laboratory reared animals were a female of 175 mm ML and 1,055 g at 252 days and a male of 150 mm ML and 1,083 g at 324 days.

Mean length measurements at hatching were: 15.0 mm total length (TL); 5.5 mm mantle length (ML); 5.0 mm mantle width (MW); 8.0 mm first arm length (AL_1); and 9.0 mm third arm length (AL_3). The measured dimensions are illustrated in figure 1. First arm length represents the shortest arm length and third arm length represents the longest because the arms are in the order of 2=3.4.1. Mantle length is the standard length measurement in most cephalopod studies. For the 20 animals reared through the life cycle in 1983, growth results are given for ML (Fig. 6), MW (Fig. 7), TL (Fig. 8), AL_1 (Fig. 9) and AL_3 (Fig. 10). Regression analyses of length data indicated in all cases that there was a distinct slowing in growth in the period of 16 - 20 weeks. Collectively, the data were best split at the 18-week period. A similar break was seen in







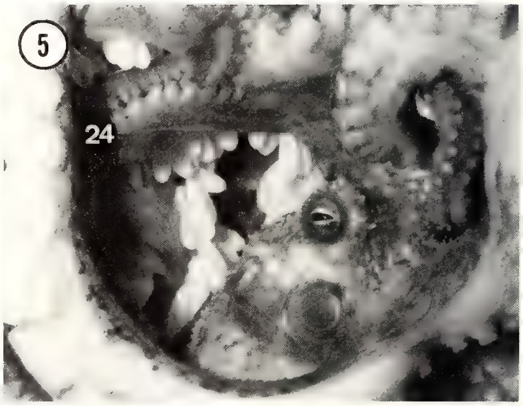


Fig. 2. Freshly laid egg clusters entwined around a central stalk, and at bottom 50-day-old eggs suspended inside a flower pot. **Fig. 3.** Egg development. From top to bottom: newly laid egg with embryo forming at right; octopus embryo before second inversion (45 days old); and dorsal and ventral views of octopus after second inversion (50 days old). **Fig. 4.** Hatching sequence. From left to right: egg capsule is split at posterior end; octopus squeezing its mantle out; only the arms remaining inside the egg capsule; newly hatched octopus. **Fig. 5.** Female octopus brooding eggs in the protective posture (Comp. 24).

analyses of the 1973 and 1981 data. Collectively, these length measurements indicate growth rates of 1.5 to 1.9% increase in body length per day during the exponential phase (d1- 126), and progressively slower rates during the logarithmic phase until senescence begins.

Analysis of wet weight increases in the 1975, 1981 and 1983 data (n = 41) revealed that growth was clearly exponential for the first 18 - 20 weeks under laboratory conditions (Fig. 11). Clearly, growth remains rapid over a long period. After 18 - 20 weeks, growth was best described by the logarithmic equation form. Full details of the 1983 weight data are given in table 2. Figure 12 illustrates changes in growth rates determined over short intervals. The highest growth rates occurred between weeks four and eight and there was an inexplicable cyclic pattern of increasing and decreasing rates during the first eight weeks. Overall, the mean growth rate over the first 18 - 20 weeks was 4.8% increase in body weight per day, which coincided well with the growth rate exponents of 4.6

Table 1. Prey organisms that *Octopus briareus* attacked or ate under laboratory conditions.

Animal	Actively Attacked	Eaten
Polychaetes		
Chaetopterus variopedatus (Renier) w/ tube	No	Yes
Hermodice carunculata (Pallas)	No	Yes
Onuphis magna Andrews w/ tube	Yes	No
O. magna w/o tube	Yes	Yes
Molluscs		
Bivalves:		
Atrina rigida Lightfoot	No	No
Chione cancellata (Linné)	No	No
Codakia orbicularis (Linné)	No	No
Donax variabilis Philippi	Yes	Yes
Gastropods:		
Busycon contrarium (Conrad)	No	No
Conus spurius atlanticus Clench	No	No
Fasciolaria tulipa (Linné)	Yes	No
Littorina sp.	No	No
Nassarius vibex (Say)	No	No
Nerita spp.	No	No
Pleuroploca gigantica (Kiener)	No	No
Prunum apicinum Menke	No	No
Pyrula sp.	No	No
Strombus alatus Gmelin	No	No
S. gigas Linné	Yes	No
Cephalopods:		
Octopus briareus	Yes	Yes
O. briareus eggs	No	Yes
O. joubini Robson	Yes	Yes
Merostome		
Limulus polyphemus (Linné)	Yes	No
Crustaceans		
Shrimps, mysids, lobsters:		
Alphaeus formosus (Gibbes)	Yes	Yes
Gonodactylus sp.	Yes	Yes
Hyppolyte sp.	Yes	Yes
Mysidopsis almyra (Bowman)	Yes	Yes
Palaemonetes pugio (Holthius)	Yes	Yes
Panulirus argus (Latréille)	Yes	Yes
Penaeus aztecus (Ives)	Yes	Yes
P. duorarum Burkenroad	Yes	Yes
Squilla empusa Say	Yes	Yes
Synalpheus brevicarpus (Merrick)	Yes	Yes
Tozeuma carolinense Kingsley	Yes	Yes
Crabs:		
Aratus pisonii (Milne-Edwards)	Yes	Yes
Calappa flammea (Herbst)	Yes	Yes
Callinectes ornatus Ordway	Yes	Yes
C. sapidus Rathburn	Yes	Yes
Cardisoma guanhumi Latréille	Yes	Yes
Clibinarius vittatus (Bosc)	Yes	Yes
Coenobita clypeatus (Herbst)	Yes	Yes
Dardanus venosus (Milne-Edwards)	Yes	Yes
Emerita talpoida Say	Yes	Yes
Gecarcinus lateralis (Freminville)	Yes	Yes
Grapsus grapsus (Linné)	Yes	Yes
Libinia erinacea (Milne-Edwards)	Yes	Yes
Macrocoeloma sp.	Yes	Yes
Menippe merceneria (Say)	Yes	Yes
Mithrax hispidus (Herbst)	Yes	Yes
Ocypode quadrata (Fabricus)	Yes	Yes
Pachygrapsus transversus (Gibbes)	Yes	Yes
Panopeus herbstii Milne-Edwards	Yes	Yes
Petrochirus diogenes Linné	Yes	Yes
Portunus spp.	Yes	Yes
Sesarma cinereum (Bosc)	Yes	Yes
Stenorhynchus seticornis (Herbst)	Yes	Yes
Uca pugilator (Bosc)	Yes	Yes
Echinoderms		
Echinaster sentis (Say)	No	No
Echinometra sp.	No	No
Holothuria floridana (Pourtalés)	No	No
Linckia guildingii Gray	No	No
Lytechinus variegatus (Leske)	No	No
Ophiothrix sp.	No	No
Oreaster reticulatus (Linné)	No	No
Fishes		
Acanthostracion quadricornis (Linné)	Yes	Yes
Adinia xenica (Jordan and Gilbert)	Yes	Yes
Cynoscion arenarius Ginsburg	Yes	Yes
Cyprinodon variegatus Lacepede	Yes	Yes
Fundulus similis (Baird & Girard)	Yes	Yes
Hippocampus erectus Perry	Yes	Yes
Menidia beryllina (Cope)	Yes	Yes
Micropogon undulatus (Linnaeus)	Yes	Yes
Monacanthus ciliatus (Mitchill)	No	No
Opsanus beta (Goode and Bean)	Yes	Yes
Pogonias cromis (Linné)	Yes	Yes
Sciaenops ocellata (Linnaeus)	Yes	Yes
Scorpaena brasiliensis Cuvier	Yes	Yes
Trachinotus caro (Linné)	Yes	Yes

and 4.8% from the exponential curve-fitting equations of the first 20 weeks in figure 11. In all cases of weight and length measurements, growth began to decrease in the period between 16 and 20 weeks, irrespective of temperature changes. The length-weight relationship was calculated from the 1983 data and is shown in figure 13; Aronson (1982) gave comparable data for field-caught *Octopus briareus*.

In summary, *Octopus briareus* growth rivals that of any fast-growing cephalopod (Forsythe and Van Heukelem, 1987) and the data here are as comprehensive as for any species (Forsythe, 1984). Previous studies indicate that temperature, prey density and sexual maturation affect feeding and growth (Boyle, 1987). Borer (1971) was able to correlate feeding in *O. briareus* with prey density and temperature under fairly natural temperature fluctuations. Studies in the open system in Miami indicated that slowing of growth could also have been correlated with a drop in winter temperature late in the year and the onset of sexual maturation. It is noteworthy that the 1983

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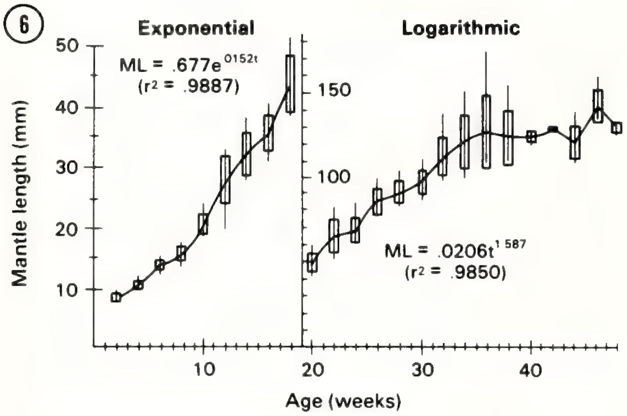

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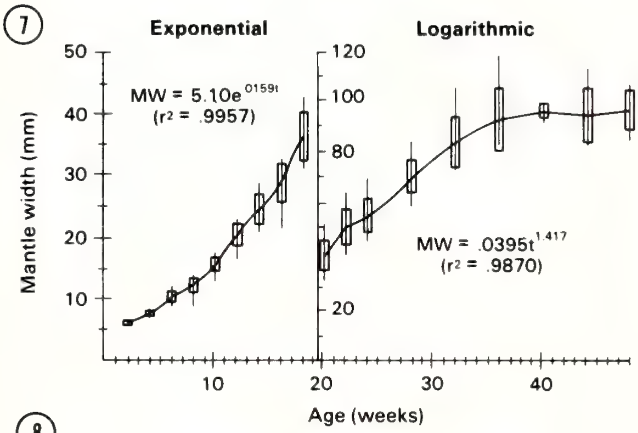

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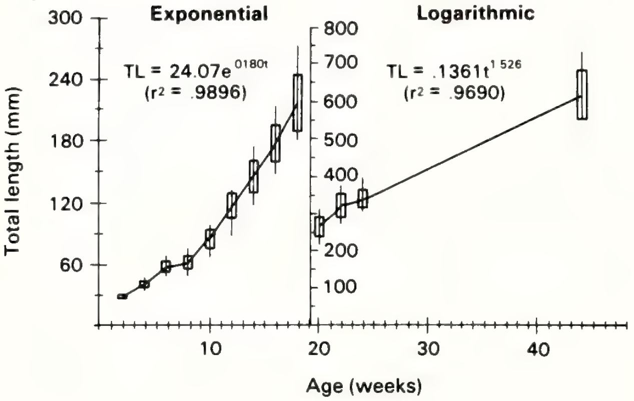

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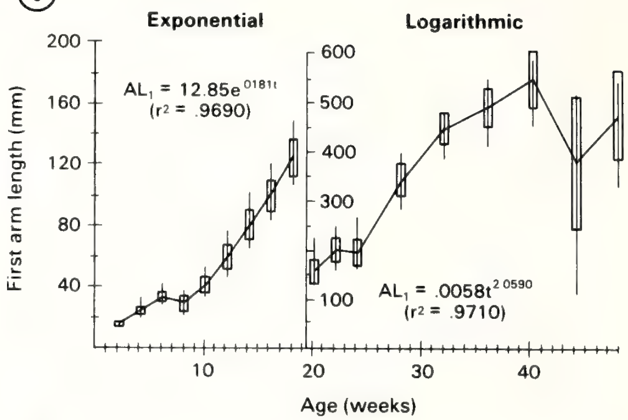

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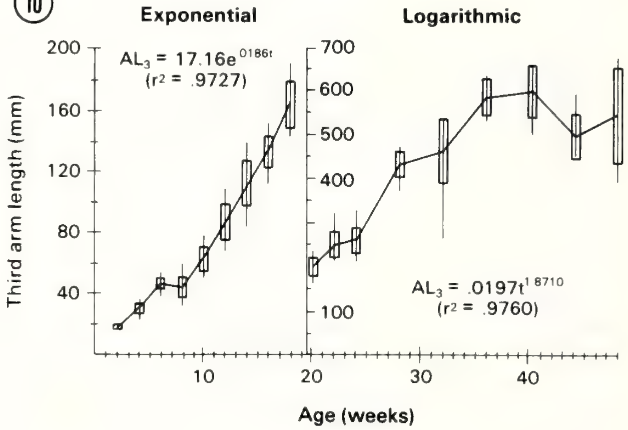

Figs. 6-10. Length versus age with mean, range and standard deviation shown for each measurement period (1983 data). Compare with figure 11. *NOTE:* The lines connect the mean values and are *not* generated from the equations.

growth data are from eggs obtained in Eleuthera, Bahamas where Aronson (1985) followed field growth of that same year class. Our laboratory reared animals grew to very large size and indicate that the small adult size of the individuals in the Eleuthera population is not limited genetically but ecologically.

ALLOMETRIC GROWTH

Typically, the slope (b) or power exponent of the length-weight relationship for animals lies between 2.5 and 4.0 (Brody, 1945; Brown, 1957). When $b = 3.0$, weight (or volume) is considered to be increasing as the cube of length (or linear size) and is indicative of isometric body growth (Gould, 1966; Ricker, 1979). When $b > 3.0$, weight is increasing at a rate greater than that required to maintain constant body proportions, thus indicating allometric body growth (Ricker, 1979). By these definitions, the slopes of the equations in figure 13 indicate that body growth of *Octopus briareus* is allometric throughout half the life cycle.

To determine more precisely if growth was occurring allometrically relative to any two of the body dimensions, the length measurements were fitted by a regression to the allometric equation $L_2 = aL_1^b$. L_1 (the independent variable) and L_2 (the dependent variable) represent the two body lengths being analyzed, a is a constant and b is the constant of allometry. Both a and b are derived from the regression (Simpson *et al.*, 1960; Ricker, 1979). When $b = 1$, growth is isometric with respect to the two lengths being compared, meaning they are growing proportionally. When $b > 1$, the L_2 dimension is growing faster than the L_1 dimension, and when $0 < b < 1$ the converse is true. In either situation growth is allometric.

The constant of allometry for each comparison is listed

Table 2. Growth in wet weight of *Octopus briareus* cultured through the life cycle in closed system aquaria in 1983. Growth rates are given as instantaneous (inst.) and those calculated from measurement to measurement and overall (ovrl.) from day 14 to each measurement. Doubling time (DBL) is the number of days needed to double in weight at the corresponding instantaneous growth rate.

Day	No.	Mean Wet Weight (g)	S.D.	Range		Growth Rate %/day		Growth Rate g/day		DBL (days)
				min.	max.	inst.	ovrl.	inst.	ovrl.	
14	20	0.20	0.04	0.16	0.27	----	----	----	----	----
28	19	0.50	0.07	0.39	0.65	6.43	6.43	0.03	0.03	10.78
42	19	0.98	0.16	0.68	1.32	4.80	5.61	0.05	0.05	14.45
56	18	1.75	0.37	1.09	2.39	4.16	5.13	0.07	0.09	16.65
70	15	3.49	0.63	2.29	5.04	4.09	5.07	0.17	0.18	14.13
84	15	8.07	1.67	5.06	11.40	6.00	5.26	0.48	0.42	11.56
98	15	14.03	3.39	9.34	22.69	3.95	5.04	0.55	0.71	17.56
112	14	25.02	5.41	17.19	36.63	4.14	4.91	1.03	1.23	16.76
126	14	45.33	11.74	30.26	72.93	4.24	4.83	1.92	2.19	16.34
140	14	68.49	19.91	40.60	113.04	2.95	4.62	2.02	3.16	23.51
154	14	121.78	40.28	70.43	210.34	4.11	4.57	5.01	5.56	16.86
168	14	183.71	48.19	117.78	296.09	2.94	4.42	5.40	8.12	23.60
182	14	281.77	71.15	175.00	438.20	3.06	4.31	8.61	12.13	22.69
196	13	362.50	70.53	267.60	519.10	1.80	4.11	6.52	14.91	38.52
211	11	450.48	98.58	335.20	698.10	1.45	3.91	6.53	17.61	47.85
224	10	546.32	108.05	414.90	805.60	1.48	3.76	8.11	20.54	46.72
238	10	645.46	128.44	492.70	971.90	1.19	3.60	7.69	23.23	58.19
252	9	707.42	145.54	528.50	1054.70	0.65	3.43	4.63	24.24	105.87
266	6	746.70	48.15	665.70	804.10	0.39	3.26	2.88	24.32	179.59
281	5	826.54	69.64	726.20	901.90	0.68	3.11	5.60	25.72	102.35
295	5	877.28	82.29	775.20	963.20	0.43	2.98	3.73	26.13	162.88
309	7	811.86	183.86	510.00	984.00	-0.55	2.81	-4.49	22.82	-125.21
324	7	869.50	239.29	432.42	1083.14	0.46	2.70	3.98	23.45	151.58
336	5	847.24	182.40	538.50	994.30	-0.22	2.59	-1.83	21.93	-320.72

in Table 3. The arms grow faster than other body parts during the exponential growth phase up to day 126. Relative to total length, the mantle length and width are growing at slower rates ($b < 1.0$), while the arm lengths (arm pairs 1 and 3) are growing isometrically with total length ($b \approx 1.0$). Consequently, arm lengths are growing faster than mantle length ($b > 1.0$) and are the major contributors to total length increases (Fig. 14). During the logarithmic phase (days 140 - 224), mantle length and width grow faster than total length ($b > 1.0$), which is partly a reflection of gonad maturation.

Therefore, the characteristic long arms of *Octopus briareus* (Pickford, 1945) are a result of positive allometric growth during the first 18 weeks of the life cycle. By comparison, Forsythe (1984) reported that *O. joubini* Robson (which is morphometrically almost identical at hatching with *O. briareus*) showed much less dramatic changes in body proportions during growth. The proportion of arm length to total length in *O. joubini* changed from 62% at hatching to 72% at maturity, whereas the same proportions in *O. briareus* changed from 50% to 78% (Fig. 14).

MORTALITY RATE IN CULTURE

Octopus briareus can be reared in individual containers throughout its entire life cycle; survival is 70 - 90% throughout the life cycle, the octopuses grow extremely fast and many of them mate normally and can lay eggs for second generation. Survival drops considerably when octopuses are mass-cultured. There is usually a slow but steady mortality throughout the life cycle (Fig. 15), although most mortality occurs before a weight of 10 gm. Forty to 60% mortality by the adult stage is common under these conditions. Causes of death vary widely by experiment, but can include premature or non-viable hatchlings, escapes, aggression, cannibalism, disease, senescence and laboratory accidents. Escapes, aggression and cannibalism are more common in *O. briareus* than in other large-egged octopus species that have been reared in the laboratory (Hanlon and Forsythe, 1985).

Table 3. Constants of allometry (b) for both growth phases calculated from allometric equations for total length (TL) relative to mantle length (ML), mantle width (MW), first arm length (AL_1) and third (AL_3) arm lengths (n=8).

Comparison	Exponential phase 14-126 Days b	Logarithmic phase 140-224 Days b
TL/ML	0.8405	1.1470
TL/MW	0.8764	1.1830
TL/AL_1	0.9909	0.9083
TL/AL_3	1.0390	0.9431
ML/AL_1	1.1300	1.2620
ML/AL_3	1.2030	1.0530

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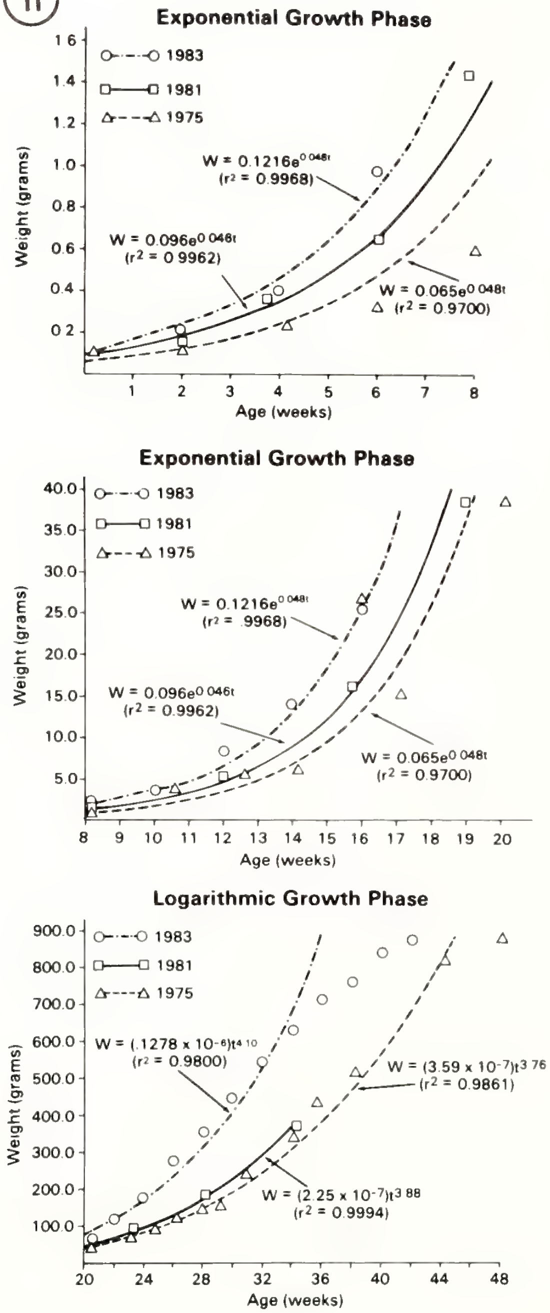

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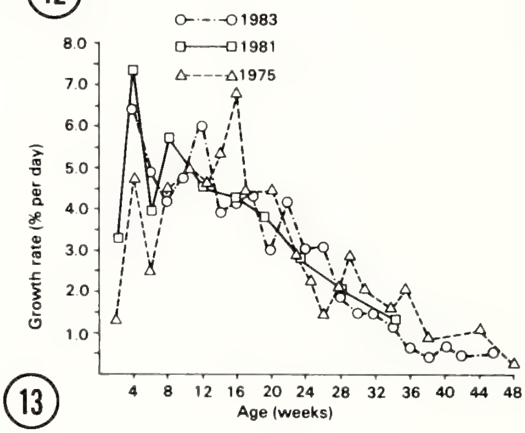

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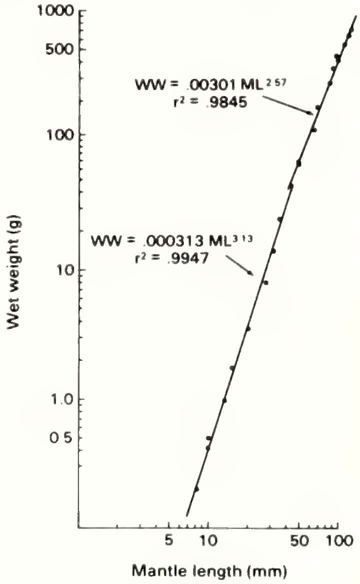

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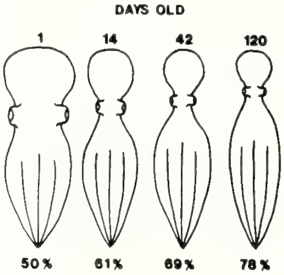


Fig. 11. Growth in wet weight versus time. The growth curves were derived from the given equations using the plotted data points, which represent mean weights. Age in days is t and the coefficient of correlation is r^2. See Table 2 for details and compare 1983 data with figures 6-10. Figures 11 and 12 reprinted from Hanlon (1983) and with permission of Academic Press with addition of 1983 data. **Fig. 12.** Growth rates expressed as percent increase in body wet weight per day. Growth rates were determined from the equation:

$$G = \frac{\log e\ Y_2 - \log e\ Y_1}{t_2 - t_1} \times 100$$

where G is the instantaneous relative growth rate, Y_1 is the initial wet weight, Y_2 is the final wet weight, t_1 is the age in days at Y_1, and t_2 is the age in days at Y_2. All calculations are from the original data in figure 11. Each growth rate represents only growth between measurement days (usually every two weeks) (Figs. 11 and 12 reprinted by permission of Academic Press Inc.). **Fig. 13.** Length-weight relationship calculated from the 1983 data, calculated separately for each growth regime. **Fig. 14.** Allometric growth. During the exponential growth phase the arms grow very fast relative to the rest of the body.

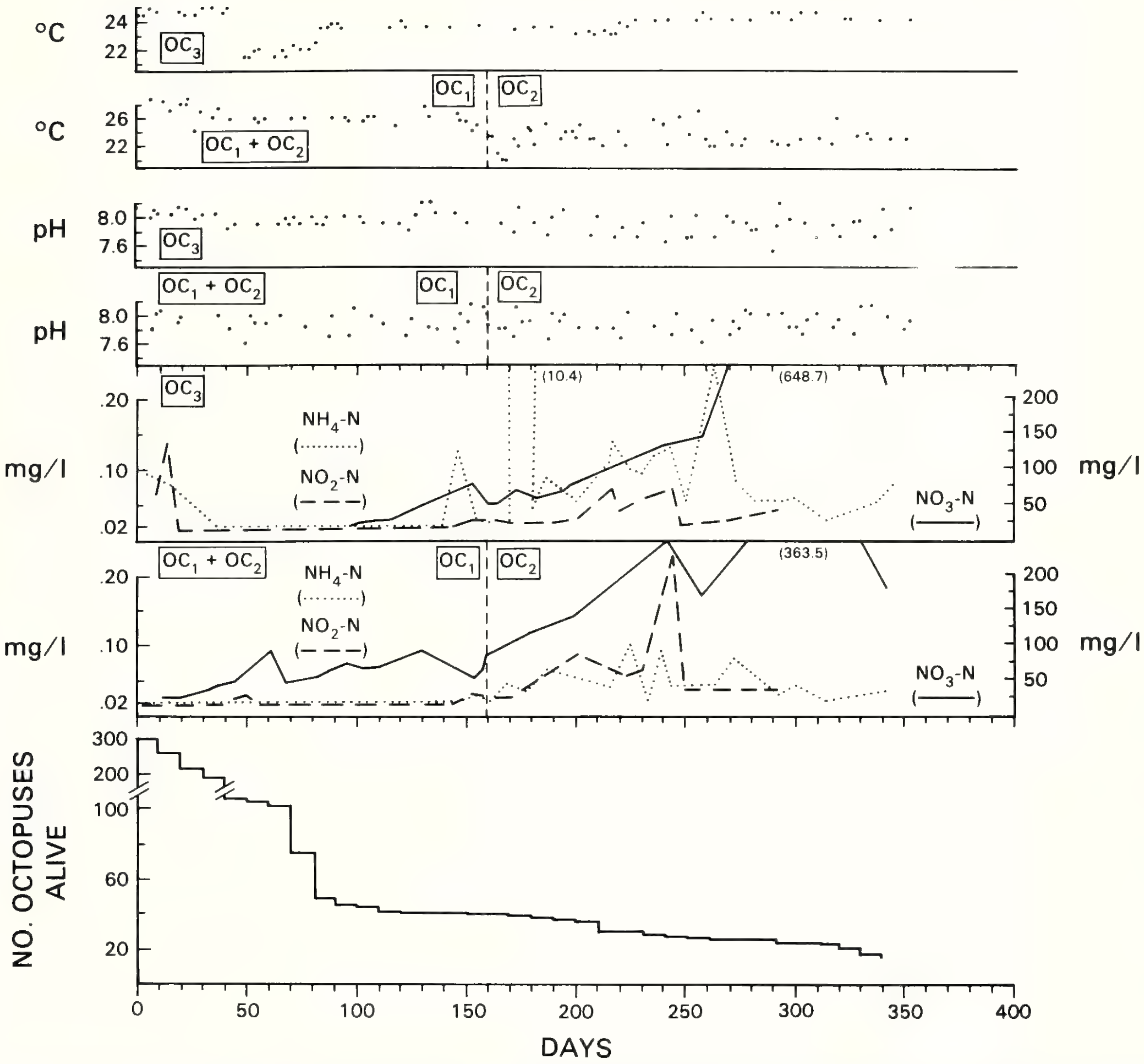


Fig. 15. Typical results of 1983 large-scale culture experiment in which the octopuses were reared in large groups. Large numbers of animals were taken out purposely on days 70 and 80. Note the high levels of ammonia, nitrite and nitrate in the latter portion of the experiment, indicating that the animals are much more hardy than previously thought. OC $_{1,2,3}$ are different tank systems.

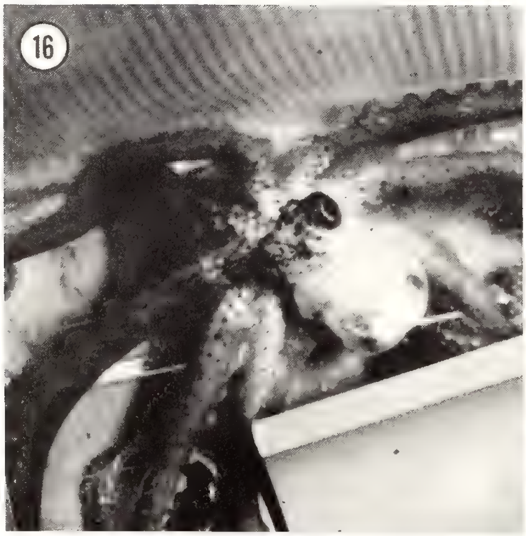
CANNIBALISM AND PATHOLOGY

Cannibalism is a common trait of *Octopus briareus* and even in the very young stages the animals will completely cannibalize conspecifics when food is in short supply. This is not merely an artifact of laboratory conditions; Aronson (1989) noted six observations of cannibalism in his field study.

Mesozoan parasites occur in the kidneys of *Octopus briareus* but do not cause mortality (Short, 1961). Fatal skin ulcers (Fig. 16) were caused by *Vibrio* spp. that occur naturally in seawater; full details of this disease can be found in Hanlon *et al.* (1984). The initial cause of skin damage was the effect of sucker marks when young animals aggregated during the young stages of group culture. Octopuses grown in individual containers in the same seawater system were free of disease. The anti-bacterial compound nifurpirinol (Furanace®) was effective in stopping the progression of the ulcers and several animals healed completely two months after treatment. Sucker scars on the mantle of laboratory reared adults and octopuses in nature do not seem to get infected similarly, indicating that larger animals could be less susceptible to secondary infection.

SENESCENCE

Senescence occurred in 10 - 12 months in all laboratory



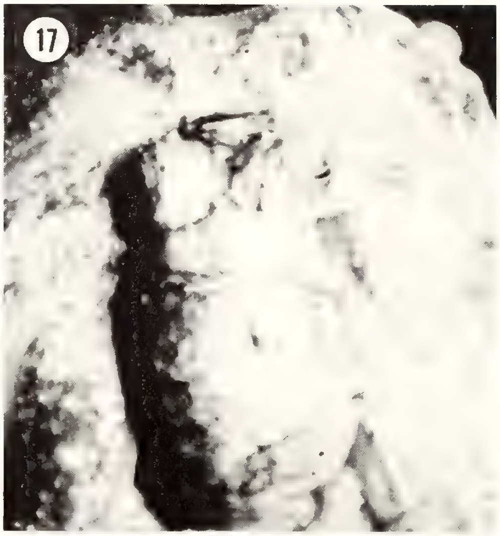


Fig. 16. One-month-old juvenile with severe skin ulceration of the mantle (whitish areas). The arms are normal. **Fig. 17.** Senescent adult octopus. Note the poor condition of the skin of the mantle.

studies, although two animals lived particularly long: one male lived 500 days in open-system culture and another male lived 492 days in closed-system culture. Both animals attained only a moderate size, and both had almost certainly mated in the time period of 190 to 200 days. In the vast majority of natural deaths males and females underwent a two to four week period of deterioration, during which feeding was sporadic and the skin, arms and internal organs degenerated (Fig. 17). In most males, this deterioration occurred at varying periods after mating and growth to a large size. In females it occurred after egg laying and brooding. The most obvious manifestation of senescence was that the skin tone degenerated and the skin became gray and the papillae were inoperable. The mechanisms of death are unknown but are probably linked to the hormone system that regulates sexual maturation (Van Heukelem, 1979; O'Dor and Wells, 1987). Rearing studies from different brood stocks in different years show consistently that the life span ranges from ten to 17 months; field data indicate the same (Hanlon, 1983). Efforts to increase longevity by feeding brooding females or rearing octopuses at constantly warm temperatures with high food availability result in the same mortality as brooding females without food or octopuses reared in open systems with normal temperature fluctuations.

BEHAVIOR

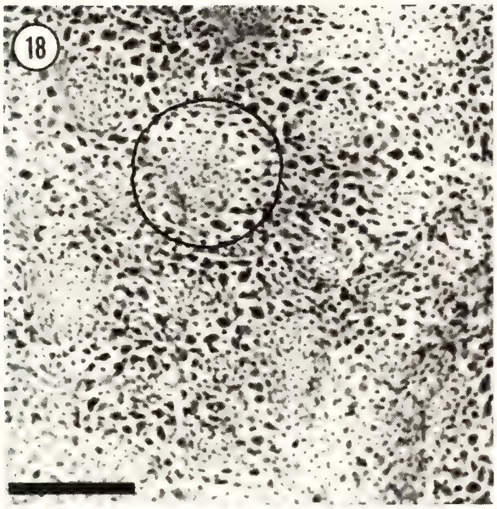
The importance of behavior in describing and understanding all activities of octopuses cannot be over stressed. Octopuses are generally solitary until they mate. Their soft bodies require that they avoid predator detection during their daily foraging for food. They accomplish this by camouflage, by operating mainly in the dark, by taking advantage of bottom relief for protection and, at last resort, by threatening predators with specific body patterns or by ejecting ink and escaping.

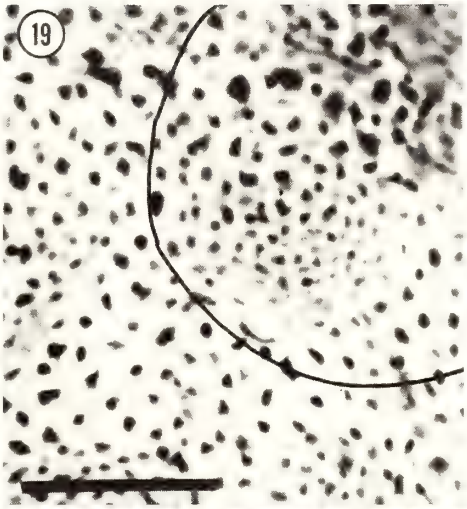
Octopus behavior is complex. The central nervous system (CNS) is large and organized into many discrete lobes (Young, 1971). Their vision is superb (Messenger, 1981) and they have demonstrated abilities of learning and memory (Wells, 1978). In *Octopus briareus* these attributes are used to compete in the high-density habitats associated with Caribbean coral reefs (Hanlon, unpub. data). Predators on octopuses are fishes and mammals (e.g. Randall, 1967; Packard, 1972).

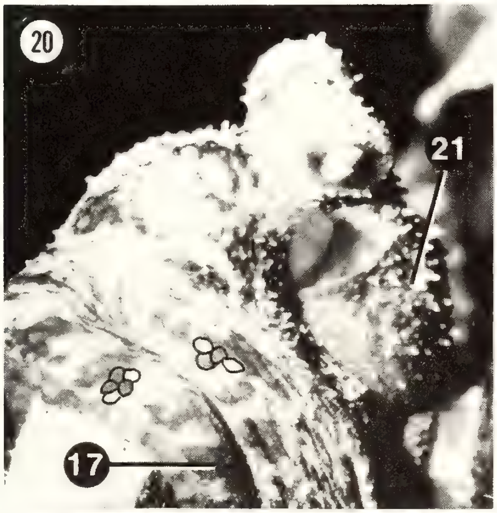
We attempt in this section to describe and explain the main facets of behavior of *Octopus briareus*. The data are based mainly upon laboratory observations (over 1400 hours) but have been corroborated with field observations throughout the Caribbean Sea (Hanlon, unpub. data). Laboratory observations were made mostly (> 60%) during the day, with numerous observations made at night with the lights on, and a few at night with a 30-watt red light. Distinctive body patterns and behaviors of *O. briareus* that are useful in species identification have been compared by Hanlon (1988).

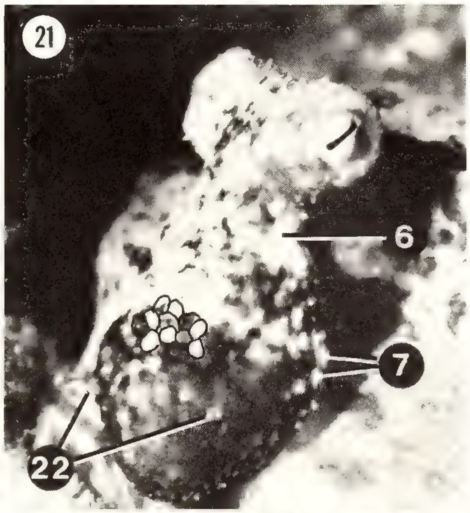
MORPHOLOGY OF BODY PATTERNS

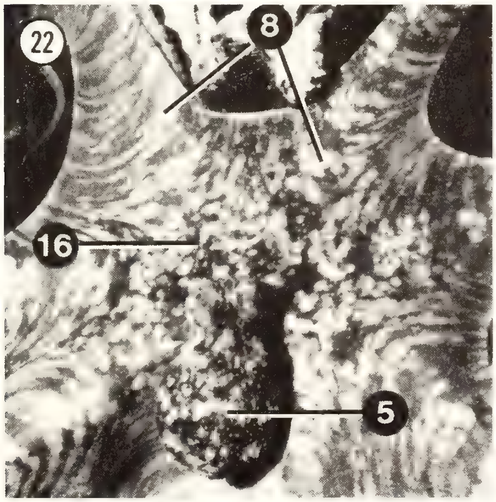
Anyone who has observed a live octopus takes immediate notice of the changing color and texture of the skin as well as the soft, supple body that can assume a variety of shapes. The appearance of an octopus at any given moment is known as a body pattern, and its expression is mediated by the remarkably well-developed eyes, CNS and skin. The octopus is almost certainly color blind (Messenger, 1981), but it can blend with its background by adjusting the expansion of its numerous, neurally controlled chromatophore organs in the dermis of the skin. The chromatophore system is regulated primarily by visual input to the eye. Together, the eyes and skin constitute a system for camouflage that matches luminance (Messenger, 1979). Below the chromatophores in the dermis is a system of broad-band reflecting cells (i.e. iridophores, reflector cells and











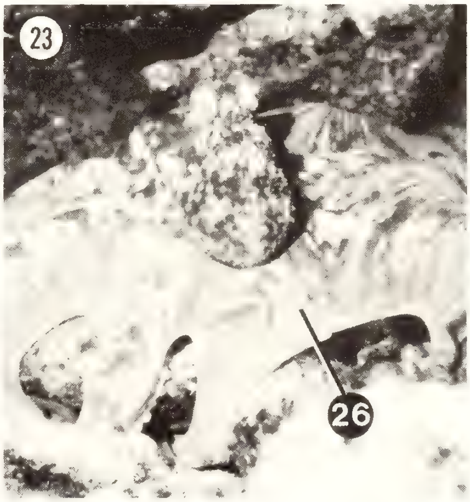


Fig. 18. Close-up photograph of the skin of an adult. Marked area indicates "visual unit" (scale = 1 mm). **Fig. 19.** Skin close-up of visual unit (scale = 0.5 mm). **Figs. 20, 21.** Adult octopus sitting on a coral head. Several examples of "visual units" are circled in ink. Note various component numbers. **Fig. 22.** Adult octopus in the Acute Mottle pattern. Note numbered components. **Fig. 23.** Large adult performing the Parachute Attack maneuver as a speculative pounce on a small coral at night off Roatan, Honduras.

leucophores) that reflects and scatters incident light of all wavelengths. Taken together, the chromatophores and reflecting cells are capable of producing a wide spectrum of visible light from the skin.

All known aspects of behavior are associated with specific body patterns. Thus, one cannot adequately describe behavior in cephalopods without describing the body patterns, many of which are species-, sex-, age- and behavior-specific. Packard and his collaborators (e.g. Packard and Sanders, 1969, 1971; Packard and Hochberg, 1977) developed a hierarchical classification in which *elements* (e.g. chromatophores) are grouped into *units* or skin patches, groups of units make up specific *components*, different components form *patterns* on the whole animal, and *patterns are reflections of the whole behavior of the animal.* Packard and Hochberg (1977) developed four general principles of patterning in cephalopods, and the interested reader should consult that paper for details. This classification of patterning has been used to describe patterning in several cephalopods including *Octopus vulgaris* (ibid.), *O. burryi* Voss (Hanlon and Hixon, 1980), *Eledone cirrhosa* (Lamarck) (Boyle and Dubas, 1981), the teuthoid squid *Loligo plei* (Blainville) (Hanlon, 1982) and the sepioid cuttlefish *Sepia officinalis* Linné (Hanlon and Messenger, 1988). For standardization, capitalization is used for the components (first letter only) and body patterns (first letter of each word).

ELEMENTS: These are the smallest visible entities in the skin that produce color or texture. In *Octopus briareus*, this includes chromatophores (three color classes: yellow-orange, red-brown, brown-black), reflecting cells and papillae. The chromatophores (Figs. 18, 19) are small (approximately 0.011 mm retracted, 0.10 mm expanded) and dense in the skin (approximately 400 per mm^2 in adults). There are also extrategumental chromatophores on the dorsal viscera of hatchlings; these expand and retract for several weeks posthatching and are a conspicuous element of patterning in young octopuses when the mantle is still translucent. The variety of reflecting cells (i.e. iridophores and leucophores) has not been studied in detail (i.e. with light and electron microscopy), but one type produces the blue-green coloration that is a distinguishing character of this octopus species. Papillae can be produced all over the body; a generalization is that there are short (1 mm) round (0.5 mm diameter) papillae, and long (3 mm) round (3 mm diameter) papillae.

UNITS: These are difficult to define in *Octopus briareus*. Packard and Hochberg (1977) originally depicted units as the

Table 4. Body patterns and their components in *Octopus briareus* (the numbered components are listed on most figures).

CHROMATIC COMPONENTS

Light			Dark
(1) Pupil margin			(9) Pupil
(2) White iris			(10) Dark iris
(3) Iris margin			(11) Dark eye ring
(4) Head bar	head & mantle		(12) Reflective eyeball
(5) Transverse mantle bar			(13) Branchial hearts
(6) White patches			(14) Extrategumental chromatophores
(7) White papillae	arms		(15) Dark hood
(8) White transverse arm bands			(16) Mottle
		arms	(17) Transverse arm bands
			(18) Dark edge suckers

TEXTURAL COMPONENTS
(19) Smooth skin
(20) Coarse skin
(21) Papillate skin
(22) Prominent mantle papillae

POSTURAL COMPONENTS
(23) Standing
(24) Protective posture
(25) Outstretched arms
(26) Interbrachial web spread
(27) Tucked in, curled arms
(28) Coiled arms
(29) Flattened head
(30) Raised head
(31) Distended mantle

LOCOMOTOR COMPONENTS
(32) Head bobbing
(33) Leaning
(34) Water jetting
(35) Inking

BODY PATTERNS

Chronic patterns (hours or days)
1. Uniform Light Phase
2. Uniform Light Blue-green Phase
3. Chronic General Mottle

Acute patterns (seconds or minutes)
Uniform Darkening
5. Acute Mottle
6. Deimatic
7. Passing Cloud

MANEUVERS
1. Parachute Attack
2. Pincer Feeding Approach
3. Side Arm Attack
4. Countershaded Swimming
5. Copulation
6. Cleaning Maneuver

static morphological array of elements in the skin (especially the chromatophores). In *O. vulgaris* there is a conspicuous morphological unit - a system of grooves that create obvious skin patches, or "chromatic units," but this arrangement is not seen in all octopuses, including *O. briareus*. The concept of a "physiological unit" can also be considered (Packard, 1982), based upon neural control of the units by motor axons originating in the CNS. In our study we limit our analysis to small circular "visual units" that are mainly physiological entities generally appearing dark or light in various components (Figs. 18-23). Each visual unit has a papilla in the center and varies in size, but there are three basic size categories: 0.5 mm diameter with approximately 80 chromatophores; 1.5 mm with approximately 700 chromatophores; and 3.0 mm with approximately 1500 chromatophores. Each visual unit also comprises an unknown number and arrangement of reflecting cells such as the leucophores that reflect the bright white seen in many components. We do not promote use of the term "visual unit" until detailed work is undertaken.

COMPONENTS: These are the recognizable and repeatable parts that constitute the whole body patterns. Thirty-five are listed in table 4 under four categories: (1) chromatic, (2) textural, (3) postural and (4) locomotor. As explained by Packard and Sanders (1971), components may be expressed in a wide variety of combinations. Some components commonly go together while others are mutally exclusive. Collectively they confer upon the animal the ability to show a highly diversified range of body patterns.

Chromatic components are those concerned strictly with color. They are conspicuous and well defined and occur repeatedly in the same relative position on the body. They are recognizable because of contrasting light and dark areas. The light components result when the overlying chromatophores are retracted and light is reflected from the underlying leucophores or iridophores. The dark components result from light that is reflected from and transmitted through the pigment granules of expanded chromatophores. Chromatic components are physiological entities that reflect selected neural activity because individual chromatophores are controlled directly from the CNS (cf. Messenger and Miyan, 1986).

The components are numbered (Table 4) and most are self-explanatory and indicated on the figures. Figure 24 depicts the arrangement of seven chromatic components that are associated with the eye. The appearance of the eye fluctuates constantly, and it can appear prominent or obliterated depending upon the combinations of these components that are expressed at any given moment. The iris can be either light (Comp. 2) or dark (Comp. 10) depending upon the degree of expansion of the iris chromatophores. The pupil of the eye always appears black. Depending upon the quantity of incident light, the pupil can appear as a thin horizontal slit or a circle. The outer perimeter of the eye is generally the same color as the head, and with expanded chromatophores it forms the Dark eye ring. The region above the eye can also be papillate (Comp. 21). In young animals, the presence or absence of expanded chromatphores on the outer eye ring determines how obvious the Reflective eyeball will appear in hatchlings. The Dark eye ring can make the eye appear larger by matching the color of the eye or contrasting with the Iris margin. The Pupil margin and Iris margin are thin rings that enhance the contrast of the pupil or eye. Some representative illustrations of components common in young *O. briareus* are shown in Figs. 25-32.

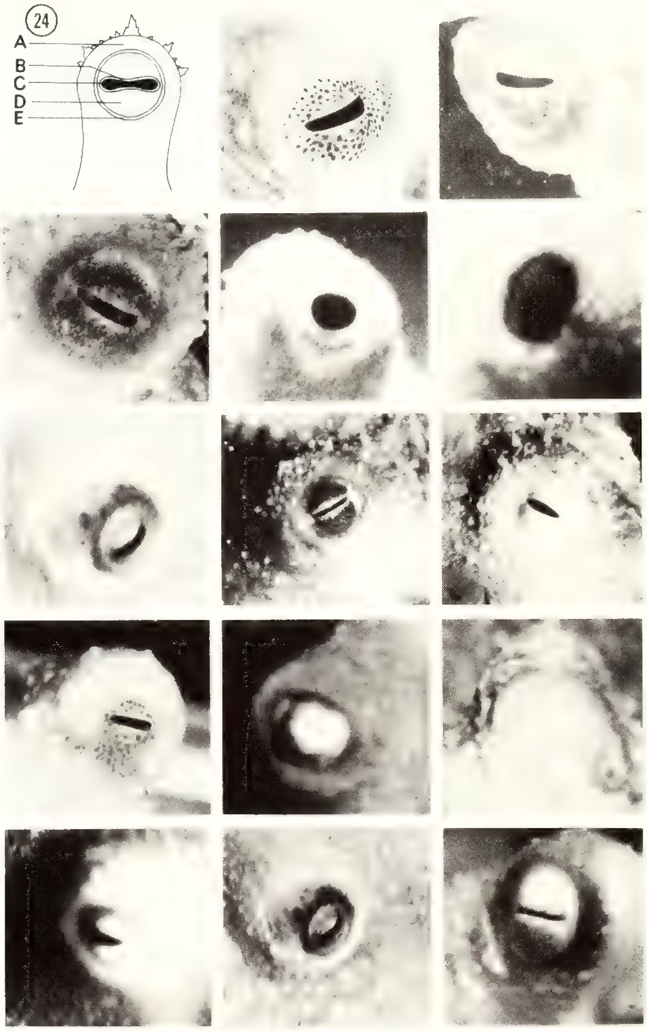
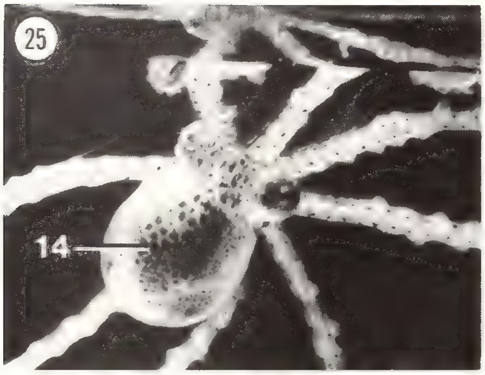
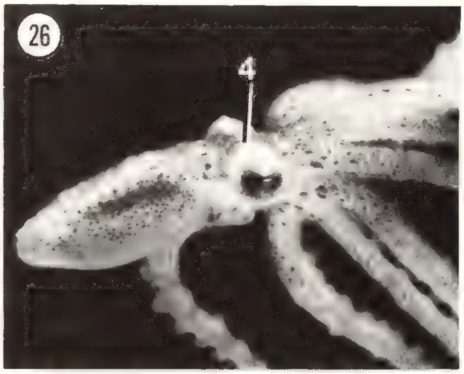


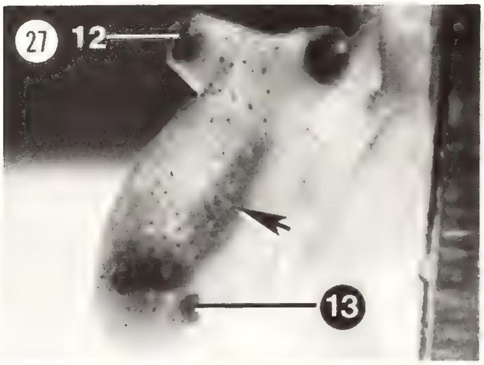
Fig. 24. The chromatic components of the eye. Note the range of expression. Not all pupils were printed horizontal. A, Dark eye ring; B, Pupil margin; C, Pupil; D, Iris; E, Iris margin.

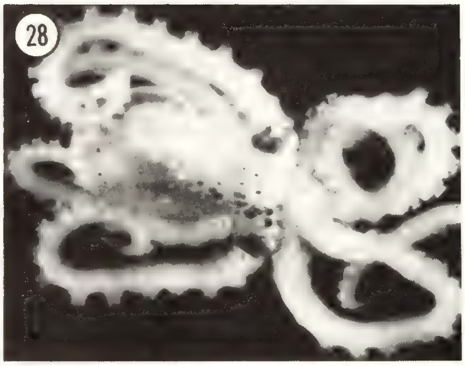
The White patches (Figs. 20-23; Comp. 6) are irregularly shaped and made up of several circular visual units in which the chromatophores are retracted. The white Head bar (Figs. 26, 29, 30; Comp. 4) consists of an irregular, transverse row of white patches between the eyes. The Transverse mantle bar (Figs. 29, 30, 33; Comp. 5) is irregular in shape and consists of a series of white patches each with a White papilla (Comp. 7). White transverse arm bands (Figs. 20-23; Comp. 8) are fairly regularly spaced and are made up of groups of White patches.

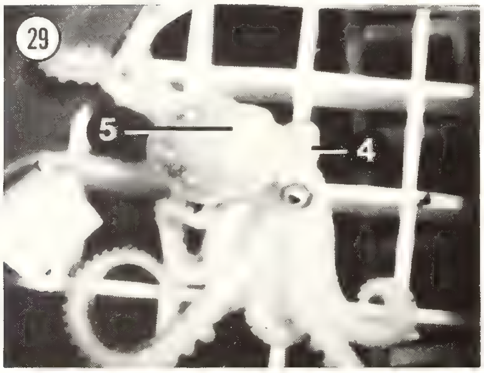
The dark components Branchial hearts (Figs. 27, 29;

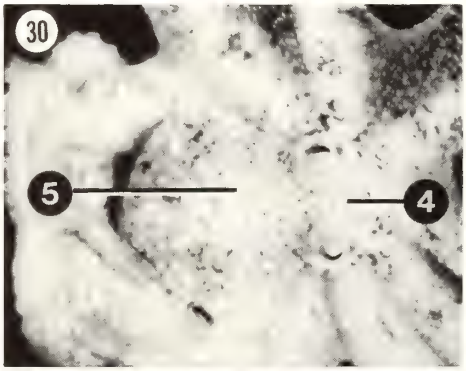


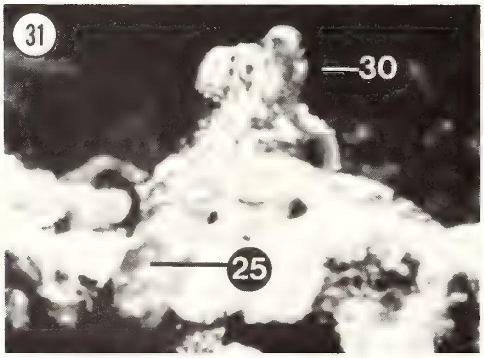












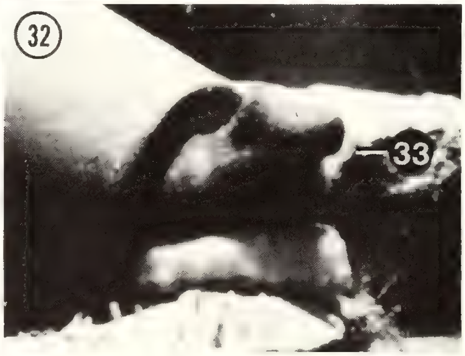


Fig. 25. Twenty-four-day-old juvenile. Note the extrategumental chromatophores (14) of the arms (two rows), head and visceral mantle. **Fig. 26.** Thirty-four-day-old juvenile. Note the newly developed Head bar (4). **Fig. 27.** Thirty-eight-day-old juvenile. Note newly developed iridophore splotches (arrow), Reflective eyeballs (12) and Branchial hearts (13). **Fig. 28.** Thirty-day-old young showing unilateral expression of chromatophores on the mantle. **Fig. 29.** Fifty-day-old juvenile in Uniform Light Phase. Note the formation of the Transverse mantle bar (5) and the Head bar (4) by aggregations of iridophore or leucophore splotches. **Fig. 30.** Two young octopuses, the one in the foreground showing Head bar (4) and Transverse mantle bar (5). **Fig. 31.** Young octopus on a reef showing Outstretched arms (25) and Raised head (30). **Fig. 32.** Young octopus in Uniform Darkening pattern showing the locomotor component Leaning (33) while it sights a prey organism.

Comp. 13) and Extrategumental chromatophores (Figs. 4, 25; Comp. 14) are evident only several weeks posthatching when the mantle is translucent. Dark hood (Fig. 34; Comp. 15), in its fullest form, includes all of the head, eyes and mantle, but can only cover the head and the area in front of the eyes. The dark Mottle (Figs. 20-23; Comp. 16) can be expressed as large circular patches with all chromatophores expanded or as irregular reticulations. The dark Transverse arm bands (Figs. 22, 23; Comp. 17) are irregularly shaped and often not well developed. The bands extend onto the web in the form of parallel dark streaks. Dark edged suckers (Fig. 35; Comp. 18) enhance the white suckers.

Most of the remainder of the components are self-explanatory or evident in the figures. The Standing posture (Comp. 23) is shown in figure 36. Outstretched arms (Comp. 25) are seen in figures 31 and 37. Tucked in, curled arms (Figs. 35, 38; Comp. 27) protect the delicate arm tips. Prominent mantle papillae (Comp. 22) are about 3 mm high (Fig. 33) and their placement is illustrated in figure 39. The Protective posture (Fig. 40; Comp. 24) is a defensive posture in which the suckers and sometimes the mouth (i.e. the animal's weapons) face an intruder, thus protecting the vulnerable head and mantle. Females brood eggs in this posture (Fig. 5). Coiled arms (Fig. 41; Comp. 28) maximize the web spread. Various postures are assumed in swimming and these are illustrated in figures 42-44. In Distended mantle (Fig. 45; Comp. 31) the mantle is full of water and the animals holds its breath. Vertical head bobbing (Comp. 32) is used during prey fixation. A typical posture with Coiled arms (Comp. 28) is shown in figure 46. The unusual Flattened head posture (Comp. 29) is illustrated in figure 47. The use of these and the other components in body patterning will be explained in the following sections.

BODY PATTERNS AND MANEUVERS: Table 4 lists those observed in *Octopus briareus*. We have listed seven basic patterns under two broad categories: chronic and acute, depending upon their duration. Chronic patterns are used for concealment, while acute patterns are used in inter- and intraspecific encounters while the octopus is out of its lair and moving on the substratum.

Uniform Light Phase (Figs. 27, 29, 35) is a chronic pattern observed frequently. It is characterized by no dark components, leaving a uniform background of white, dull yellow or brown; usually there are uniformly raised papillae. Uniform Light Blue-green Phase is seen in the field over light sandy patches around reefs. No chromatophores are expanded, and the resulting light blue-green tint has a glowing effect that is a result of reflection from the various reflecting cells. All papillae are usually raised uniformly producing Coarse skin. This same blue-green tint is present over much of the body during the Deimatic pattern. Chronic General Mottle (Figs. 20-23, 31) is an extremely common pattern that is variable in form. The head and mantle have more circular light and dark patches while the arms are characterized mainly by Transverse arm bands. In general, laboratory reared octopuses showed less chromatic expression than field-caught animals, and field-caught animals maintained for long periods showed less-intense patterns over time.

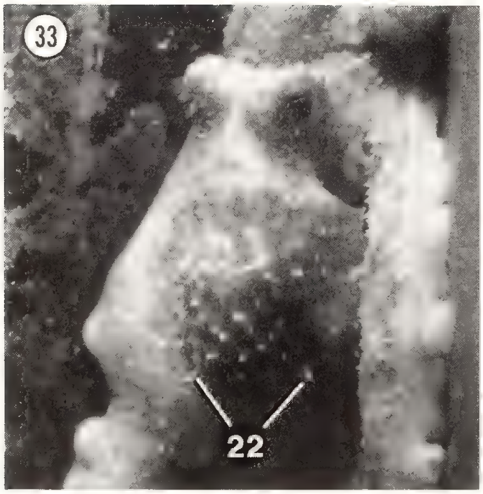
Acute patterns are by definition short-lived and can be generally regarded as immediate responses to stimuli (e.g. predators, prey, conspecifics). Uniform Darkening (Fig. 37) is characterized by the uniformly maximal expansion of all chromatophores, resulting in an overall dark brown coloration. The pattern results when the octopus is stressed, as when approached closely by another octopus, a predator or a human observer. The skin texture can be either smooth or sculptured by varying degrees of raised papillae. Variations include the presence of white eyes (roughly one-fourth of the time) or some very dark mottle in the form of dark reticulation. A more striking variation is a blue-green metallic sheen that apparently is produced by the expression of iridophores on raised papillae.

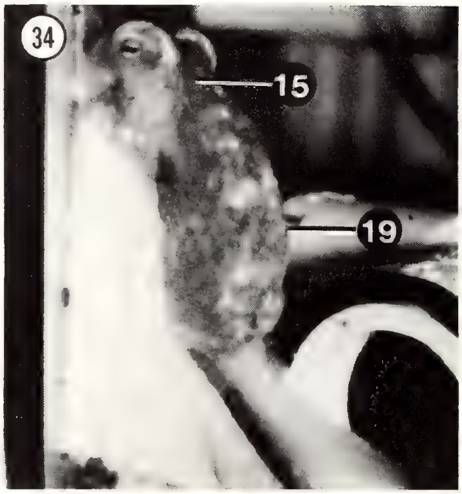
Acute Mottle (Fig. 22) is a variegated pattern that is characterized by the components Mottle, White patches, Papillate skin and Interbrachial web spread. It is often accompanied by dark eye components. The pattern is used when the octopus is startled by a nearby object such as a large prey organism, a predatory fish, another octopus or a human observer. In some behavioral contexts, this pattern can be considered a precursor to the Deimatic pattern.

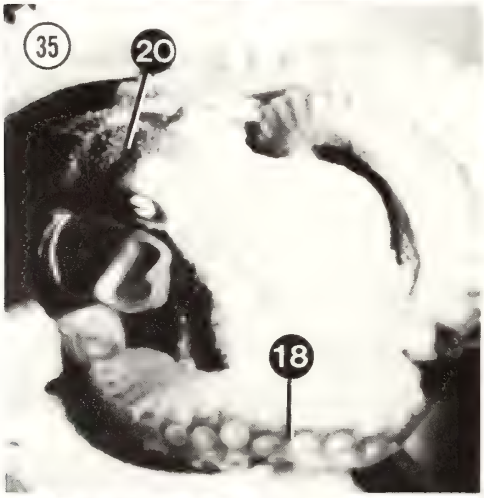
The Deimatic pattern (Fig. 41) is similar in form and expression to that described for other octopods (first coined as "Dymantic" by Young (1950) to mean warning or frightening display, but deimatic has the same root and is in wider use). The octopus flattens its head (Comp. 29) and mantle dorso-ventrally, the arms are tucked in and curled (Comp. 28) and the interbrachial web is spread slightly (Comp. 26). Concurrently the entire body surface turns pale white except for the Dark eye ring, Dark iris and expanded Pupil. Partially raised papillae form Coarse skin. This display is elicited only by a very sudden, intense, close rush by a large object or predator. The intensity of the pattern depends upon that of the stimulus as well as the reaction of individual octopuses. In situations of increasing intensity, the order of appearance of the components is: (1) expanded Pupil, Dark iris and Dark eye ring; (2) Flattened head; (3) Arms tucked in, curled; (4) paling of arms and web; and (5) complete Deimatic.

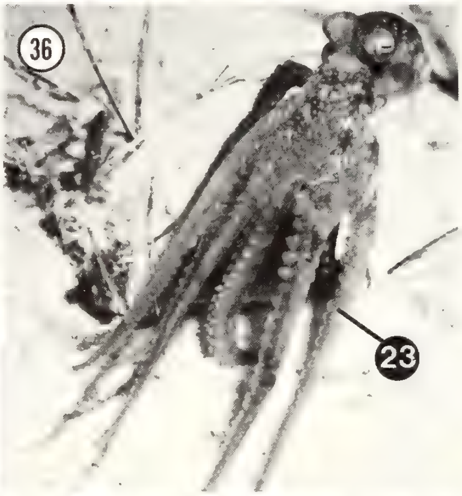
Passing Cloud (Figs. 38, 46, 48) is a dynamic pattern in which the interbrachial web is spread (Comp. 26) to its fullest and the arms are coiled (Comp. 28) upwards to present the greatest possible surface area. The body is held in this posture while the octopus glides forward slowly. Simultaneously, a unilateral chromatic effect occurs as alternate clouds of dark brown and white, originating at one eye, travel outward to the periphery of the mantle, web and arms. New waves originate at the eye and side of mantle simultaneously every second, and it takes about 1.5 secs for each wave to reach the arm tips. This pattern is always shown laterally towards another octopus and can last several minutes and be repeated many times in succession.

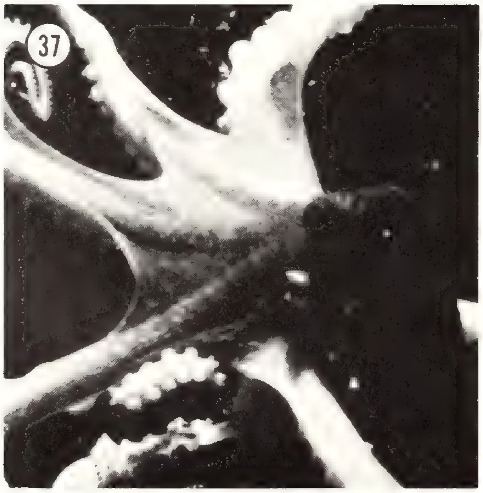
Unilateral variations result when a different pattern is present on each side of the body. Generally the side toward a stimulus is dark while the side away is light. Newly hatched octopuses also can do this (Fig. 28). This pattern resulted when either a very large crab or another octopus was in the











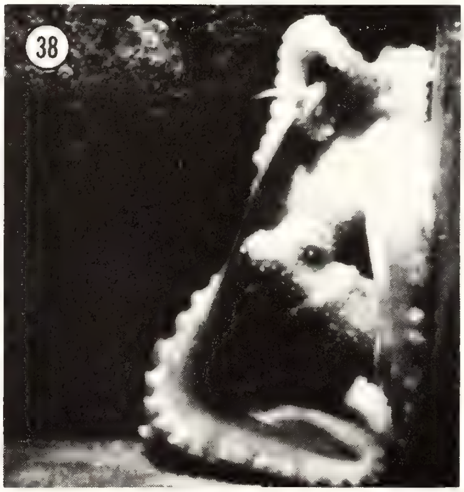


Fig. 33. Laboratory adult in a light brown Uniform Light Phase. Note two of the three Prominent mantle papillae (22). **Fig. 34.** Expression of Dark hood (15) while sitting in the raised head posture with Smooth skin (19). **Fig. 35.** Adult octopus in Uniform Light Phase. Note Dark edged suckers (18) and Coarse skin (20). **Fig. 36.** The postural component Standing (23) in a sand/seagrass area off Eleuthera Island, Bahamas. **Fig. 37.** The acute pattern Uniform Darkening and an example of Outstretched arms (25). **Fig. 38.** The Passing Cloud pattern, with a wave of expanded chromatophores passing over the arms, which are held tucked in and curled (27).

same tank with an octopus (Fig. 48). The former instance was observed 51 times; however, in two instances the opposite reaction occurred - the dark side was away from the stimulus. In one instance when a large crab was put in the tank, the octopus showed the chromatic components of Deimatic toward the crab, while showing Uniform Darkening on the other side.

Six behavioral maneuvers are noteworthy. The Parachute Attack (Figs. 49, 50) is associated with foraging and feeding. Sinel (1906) first described this motor action pattern in which the octopus "rises above its victim, and with tentacles so out-stretched that the web that joins them part of their length forms a parachute, it descends like a cloud on its victim." The general body pattern is Dark hood and white arms with smooth skin. These chromatic and textural components of the pattern appear just when the octopus has positioned itself above the prey and is beginning to descend upon it. Upon descent, the arms and interbrachial web are spread rapidly in parachute fashion, and the octopus settles on the prey and entangles it; the octopuses then immediately went to Uniform Darkening. Several variations were observed (Fig. 23; Hanlon, unpub. field data).

In the Pincer Feeding Approach (Fig. 45) the octopus is in a brown Uniform Light Phase, often papillate (Comp. 21). This maneuver is used to seize prey. The second pair of arms curve forward during the approach, and the fourth pair extend forward from underneath. The mantle is distended (Comp. 31) while the octopus holds its breath and moves toward the prey. The prey is grabbed in one motion as the pincer (arms 2) is closed and the fourth pair of arms shoots forward.

Side Arm Attack is used when prey are close. The arms on the side toward the prey coil back, with the suckers outward. Three or four arms extend rapidly above the prey then grasp it and pull it into the web. The body pattern is usually Uniform Darkening with Coarse skin.

During countershaded swimming in a backward direction (Fig. 42) the dorsal body surface is in brown Uniform Light Phase while the ventral surface is pale. The skin texture is coarse (Comp. 20) and iridescence is usually present from the reflecting cells. This pattern provides the necessary components for effective countershading of a swimming organism (Cott, 1940).

Mating behavior and copulation (Figs. 51-55) were observed and three postures were noted: (a) the male most commonly sat atop the female with his arms and interbrachial web covering the female's mantle and head, and (b) occasionally the female rotated around from her posture described in (a) until the oral surfaces of her suckers were against the oral surfaces of the male's suckers, (c) the male and female sat about 10 cm apart while the male extended his hectocotylized arm toward the female. During copulation the male's hectocotylus was inserted into the female's mantle cavity. Coloration and skin texture were variable. Brown Uniform Light Phase and Chronic General Mottle were the commonest patterns. During two matings the males turned pale white and showed Dark hood (Comp. 15) for short periods. Iridescence on the skin was common in all patterns.

Three Cleaning Maneuvers were observed. Commonly an octopus would shed the sucker discs by twirling its arms against the body and blowing them away with jets of water. A second maneuver was performed by females after mating; they would rapidly move the arms inside and on the outside of the mantle. Finally, females cleaned eggs in their lair by continually grooming the egg capsules with their arm tips.

ONTOGENY OF PATTERNING

Figure 56 gives the times of appearance of the components, patterns and maneuvers of *Octopus briareus* cultured in the laboratory. At hatching, there are no iridophores or leucophores evident in the skin (they begin to appear at two

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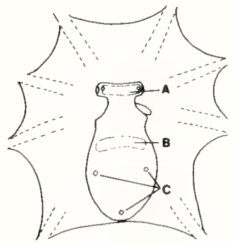

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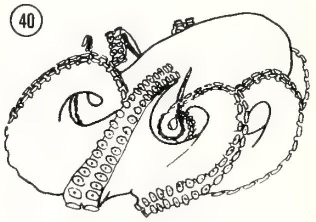

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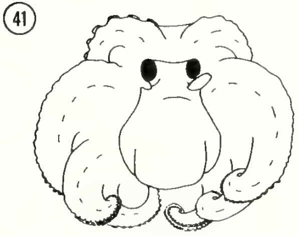

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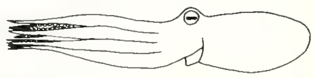

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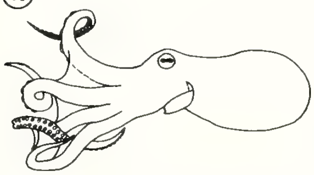

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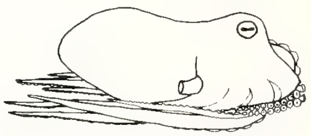

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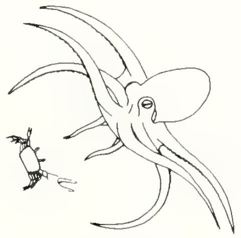

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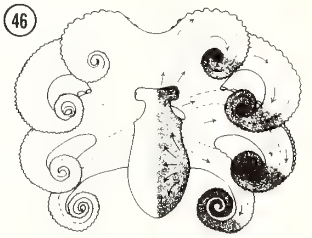
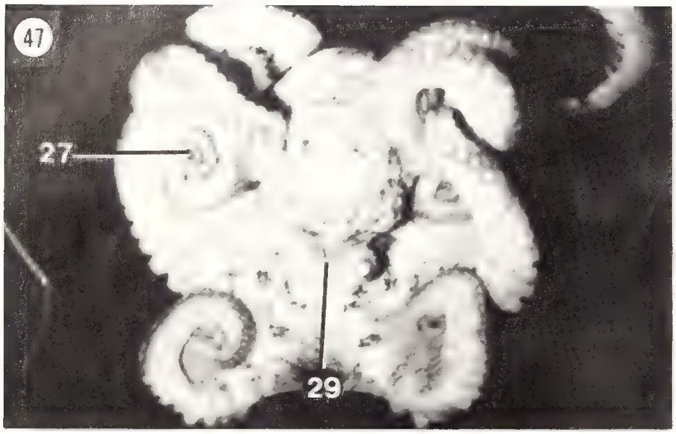
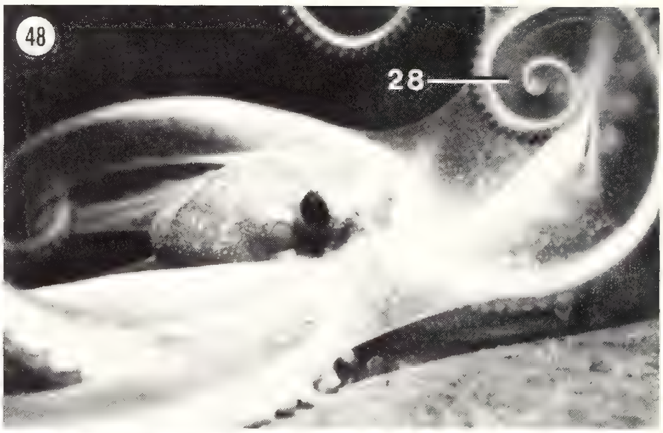
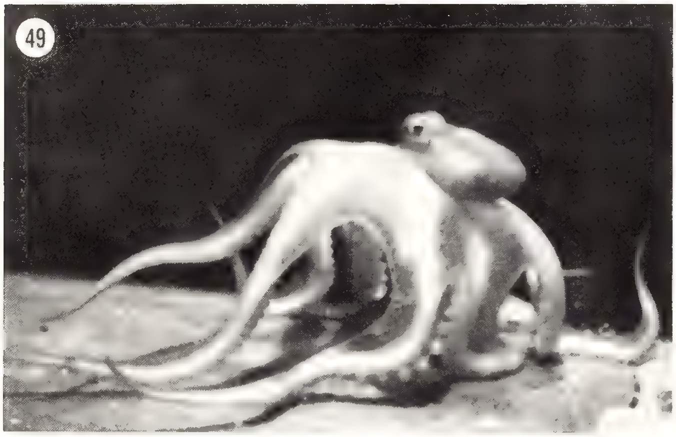


Fig. 39. Diagrammatic representation of: A - Head bar, B - Transverse mantle bar, C - Prominent mantle papillae. Two prominent eye papillae are also indicated. **Fig. 40.** Protective posture. **Fig. 41.** Deimatic pattern. **Fig. 42.** Backwards swimming. **Fig. 43.** Backward medusoid swimming. **Fig. 44.** Forward swimming. **Fig. 45.** Pincer Feeding Approach to a small crab. **Fig. 46.** The acute pattern Passing Cloud being shown unilaterally on the right. Stippled areas indicate successive waves of chromatophore expansion.







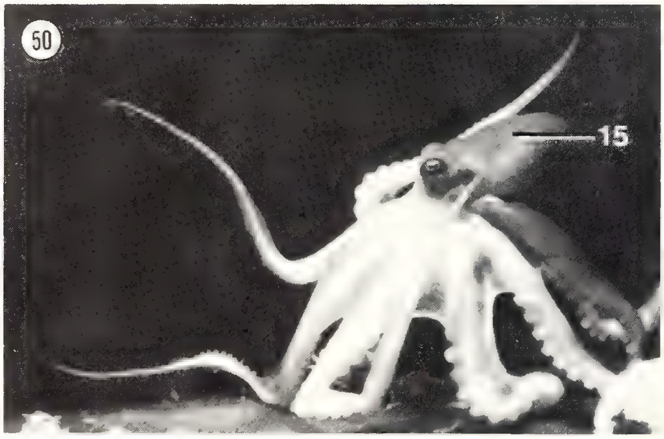


Fig. 47. Chronic General Mottle in a laboratory reared adult reared in isolation. Note Flattened Head (29). **Fig. 48.** The Passing Cloud pattern being shown unilaterally (on the animal's right side) in an animal approximately 200 days old. **Fig. 49.** The Parachute Attack in a young octopus (about 60 days old). **Fig. 50.** The Parachute Attack maneuver onto a crab in an animal 144 days old; note Dark hood (Comp. 15).

weeks) and the chromatophores are relatively sparse. Therefore, patterning is limited for the first two months or so. During this early period the Extrategumental chromatophores are important, as are the Reflective eyeballs and Branchial hearts.

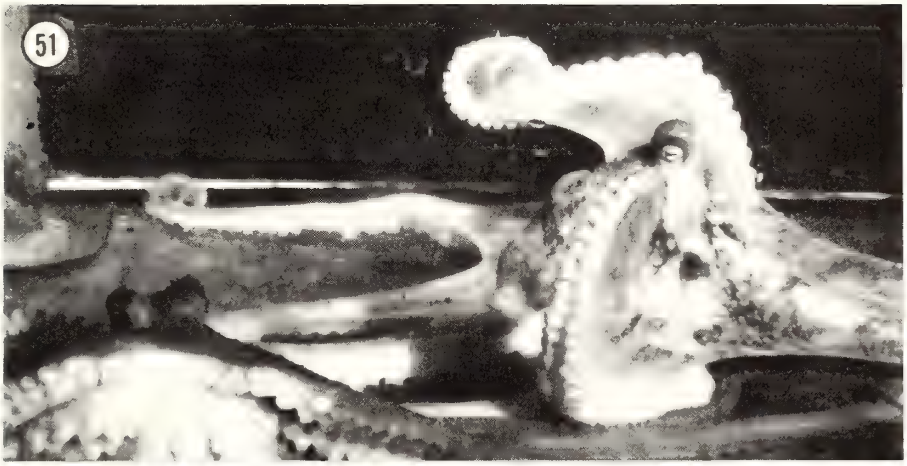
Newly hatched *Octopus briareus* appear to be restricted to four general body patterns. The first is the chronic pattern Uniform Light Phase in which the skin is translucent white, the eyes are prominent and silvery-blue, the visceral organs appear pinkish through the mantle, and the dark Branchial hearts show through the mantle and produce the effect of two false eyespots at the posterior end of the mantle. After approximately four weeks the mantle becomes thicker and more opaque, and Uniform Light Phase becomes more adult-like in appearance because the internal organs are not obvious. This pattern is common when young animals rest on a light or white object and when they are swimming.

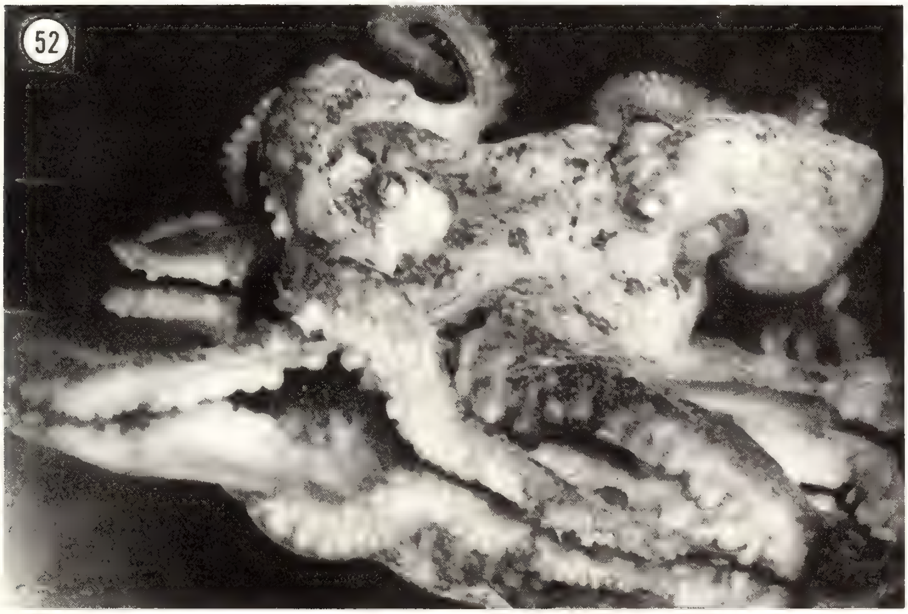
The second chronic pattern is characterized by the full expansion of the Extrategumental chromatophores on the arms and viscera (Figs. 4, 25) while most or all of the other chromatophores on the body are retracted. This pattern was most often seen when the animal was sitting on a dark object or when the octopus was moderately excited upon sighting a moving object nearby.

The third common pattern was Uniform Darkening in which all chromatophores were expanded maximally. The overall color was dark brown and the pattern rarely lasted beyond two minutes. This pattern was observed when the octopus was very excited, as when attacking a crab or when startled by a nearby object.

The fourth pattern observed in animals younger than three weeks was unilateral Uniform Darkening. The dark patterning was always seen on the side of the octopus facing another octopus or a larger crab that had been put in as a prey organism.

Some gradual changes take place between days 20 and 50. The number and density of chromatophores begins to increase and papillae develop at about day 30. The first to appear are single large papillae above each eye. By day 30 some iridophore cells first appear on the mantle as small (0.5 - 1.0 mm) isolated patches of reflective silvery-blue (Figs. 27-29). They then soon appear over the heads and arms, and groups of them begin to form the chromatic components Head bar, Transverse mantle bar and White transverse arm bands. An example of a small animal just at this transition can be seen in figure 29. A modified form of Passing Cloud has been





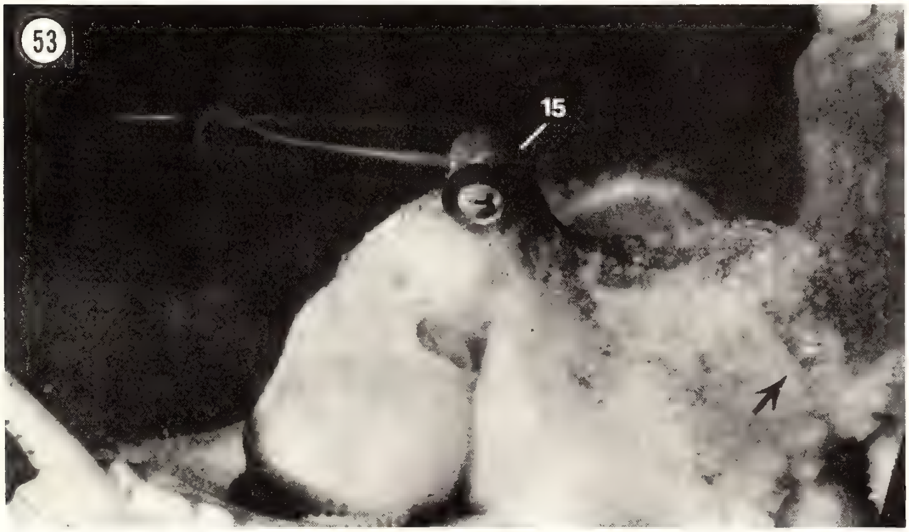
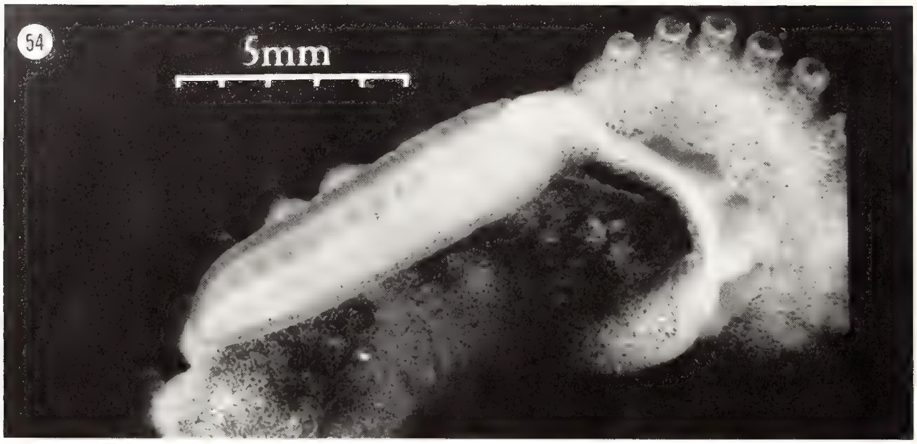


Fig. 51. Male (right) approaching a female just prior to mounting her. **Fig. 52.** Copulation. Male (right) mounting the mantle of the female. **Fig. 53.** Copulation. Male (left) showing incomplete Dark hood (15), covering the female (arrow) with the interbrachial web.



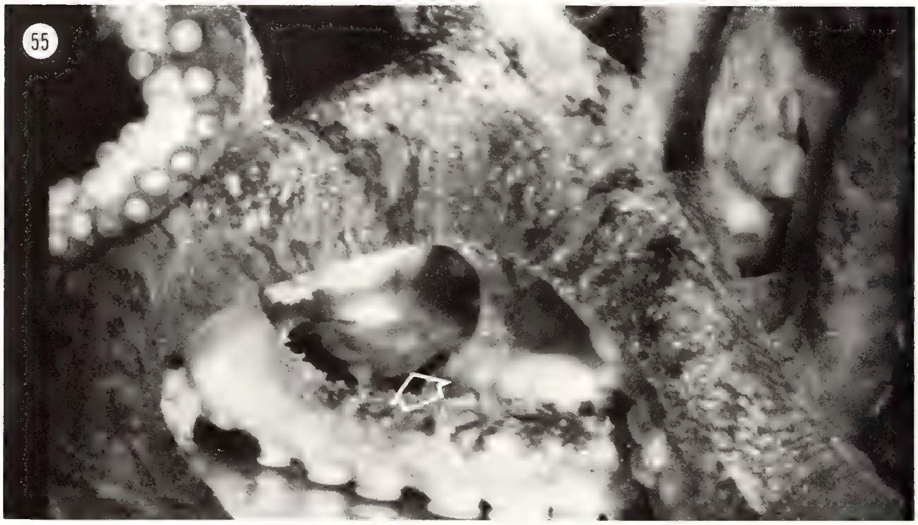


Fig. 54. Hectocotylus, third right arm modified for spermatophore transfer. **Fig. 55.** Copulation. Male is at the top and female at the bottom. Arrow indicates the hectocotylus of the male inserted into the female's mantle cavity.

seen as early as 30 days. The various components of the eye generally begin to appear between days 40 and 60. The Deimatic pattern is fully expressed at about day 100 and the typical form of Passing Cloud was not observed until day 210. However, it is likely that the animals are capable of expressing it before this time.

Copulation was not seen before six months of age. At the end of the life cycle senescence sets in and the skin begins to deteriorate. Most of the components and patterns are affected during senescence, and the common body pattern at this period is a variant of Uniform Light Phase.

LOCOMOTION AND EXPLORATORY BEHAVIOR

Octopus briareus moves by four principal methods: crawling, backward swimming, backward medusoid swimming and forward swimming (Figs. 42, 43, 44). Hatchlings are capable of crawling and backward swimming. The animals usually only swim when they are excited, and they do so in the acute pattern Uniform Darkening and often squirt three or four pseudomorphs of ink as they move backwards. Medusoid swimming and forward swimming were only observed later in the life cycle.

Exploratory behavior was common in octopuses of all ages. When an octopus is placed in a new tank or an object is placed in its home tank, the animal will usually first withdraw into the Protective posture and then soon investigate new objects by extending one or several arms cautiously. The arms can stretch a great distance and the animal is thus able to use tactile and chemosensory organs in the suckers to obtain information about new objects. Eventually the animal will touch all objects in its tank and move around to investigate them more carefully. Octopuses also use vision in exploratory behavior. They will often lean in the direction of interest to obtain better sight of an object before leaving their lair.

INTRASPECIFIC INTERACTIONS

Octopus briareus is a solitary animal for most of its life cycle. During the first few weeks posthatching, the young animals tolerate conspecifics and sometimes even aggregate in group-culture conditions. However, they soon become in-tolerant of conspecifics and cannibalism is common, especially during times of food shortage. When the gonads are ripe the animals will readily mate, but they then separate and do not form permanent mating pairs.

AGONISTIC BEHAVIOR: There is no evidence from laboratory rearing that young octopuses are territorial or maintain a permanent home. From hatching, octopuses seek shelter such as empty shells, but *Octopus briareus* is not strictly nocturnal and can be seen moving about feeding both during the day and night. Young animals have been observed feeding on the same piece of shrimp meat. Intraspecific aggressive behavior was first evident at five to six weeks of age. The first interaction was observed at day 42 when two small octopuses fought each other for five seconds. They both remained in the Uniform Light Phase pattern with their arms folded backward and interbrachial webs spread, and moved forward bringing the buccal masses together. In a similar instance, two octopuses of the same age approached each other in the Uniform Darkening pattern and extended two arms each towards each other. In some cases, an intruder was able to remove an octopus from its den by grappling with it. Fighting over food was common, especially during poor food availability or when the animals were approaching two months of age. For example, one young octopus was observed to pull the food from the web of another and then return to its den. The octopus that lost its food followed the first to the den and was attacked, with the result that its fourth right arm was torn off. Some form of hierarchy was apparent, and size and aggressiveness were probably key elements in its structure.

By two months of age there were some examples of a dominance hierarchy based upon size. The largest animals appeared to have the primary choice for den selection and feeding. This hierarchy remained constant when the animals were moved to new surroundings.

Rearing conditions strongly affect the quality and quantity of intraspecific interactions. If the animals are well spaced and there is an excess of hiding places and food, then interactions are not numerous or violent. Under more natural conditions the majority of interactions between octopuses do not end in fighting, but in displays and stylized attacks.

The acute pattern Passing Cloud appears to be used in establishing dominance. If an octopus does not respond to the Passing Cloud pattern, then the displaying octopus will often touch the other. In many cases this results in the subordinate animal fleeing or moving into the Protective posture. In other cases, a bout can ensue in which the octopuses entangle their arms attempting to maneuver on top of one another. In this position the eventual winner will wrap its arms and web around the mantle to restrict breathing. Sometime the attacks are made in a side-arm fashion with only two or three arms from each animal engaging in the bout. In some cases, the subordinate animal will autotomize an arm to facilitate rapid escape and the victor may eat the captured arm. After intraspecific bouts, it is not uncommon for circular gray wounds to be left on the mantle, presumably from the effect of the suckers.

There was one documented instance in which the dominant/subordinate relationship reversed over time. A male and female had been reared in the same tank from hatching to 100 days. Both had the circular scars on the body indicating that bouts had taken place, but no dominance was observed in either animal. Within several days, however, the male became strongly dominant, feeding first and causing the

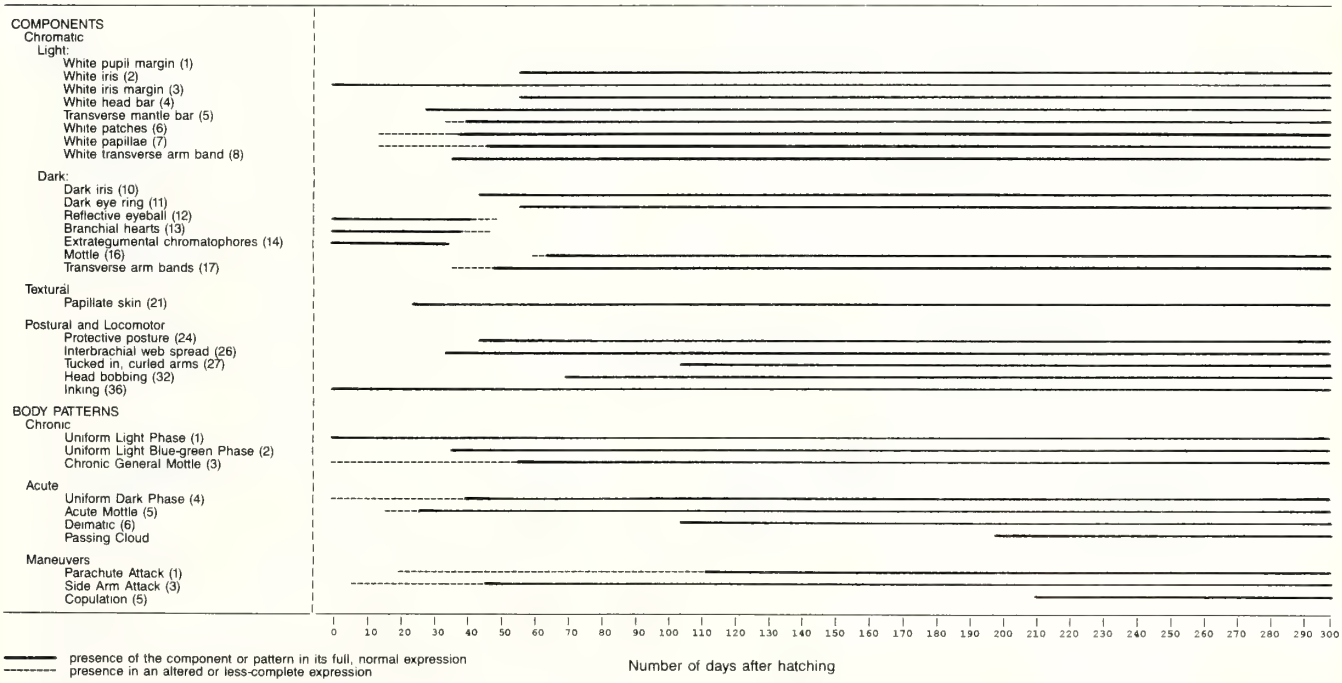


Fig. 56. Development of patterning in *Octopus briareus.*

Table 5. Visual antipredatory adaptations of *Octopus briareus* (see Table 4 for pattern descriptions).

Adaptive coloration and behavior	Body pattern	Purported effect
Primary defense Ψ - concealment from predators		
nocturnally active	all patterns	harder to see at night
remain motionless	all chronic patterns	predator is not attracted by motion
general color resemblance*	all chronic patterns	match substrate
countershading*	Uniform Light	blend with water column
disruptive coloration*	Chronic General Mottle	obliterate body form
concealment of shadow*	all chronic patterns	blend body outline with substrate
Secondary defense Ψ - make a predator hesitate		
flash behavior*	*Inking*	predator is startled and loses sight of prey
	Deimatic	pattern, posture change and apparent size increase bluff predator
	Uniform Darkening	pattern change confuses predator
	Passing Cloud	rapid color change confuses predator
	Acute Mottle	bold pattern change confuses predator
	Protective posture + *Water Jetting*	show the weapons, protect vital organs and startle predator
flight*	Uniform Darkening +*Inking* + *Jetting*	predator is startled and loses sight of prey
Tertiary defense - misdirect a predator's attack		
deflective marks*	*Branchial hearts*	misdirect predator's attack with false eyespots
diversion behaviorΨ	Uniform Darkening + *Inking* + *Jetting*	predator attacks ink blob, becomes disoriented and loses sight of prey

terminology: *Cott, 1940
ΨEdmunds, 1974

italics: components of patterns

female to relinquish captured crabs. However, during the next 30 days the female grew faster, became larger and subsequently became the dominant member of the pair. Other factors may have been involved such as a hormone change in the female, whose gonads had enlarged during this time.

REPRODUCTIVE BEHAVIOR: Mating has been observed 12 times in the laboratory and once (Hanlon, 1983) in the field. In all cases there was little or no courtship behavior, mating appeared to be male dominated, and both males and females would mate multiple times with different partners. Animals that had been reared in isolation would readily mate when placed in a tank with another mature octopus. The typical mating encounter was as follows. After being placed together in the same tank, the male would advance across the aquarium (Fig. 51) and climb on top of the female, sitting on top of her mantle with his arms draped around the mantle and head (Fig. 52). The interbrachial web between the male's first pair of arms often covered the female's eyes (Fig. 53). Most matings lasted 30 to 80 mins, but in two cases mating lasted 150 and 180 mins. During this time the male's hectocotylized third right arm (Fig. 54) would eventually be inserted into the mantle cavity of the female (Fig. 55) and a very long spermatophore (sometimes longer than the mantle length) would be transferred to the oviduct of the female. Sometime during mating it would not be unusual for long fragments of spermatophores to be seen floating in the vicinity of the octopuses. The female would occasionally struggle during mating, but termination only occurred when the male released her and the two would part quickly. Counts of ventilation rate of both partners were made to see if there were increases associated with transfer of spermatophore to the oviducts (see Wodinsky, 1973 for *Octopus vulgaris*). Five pairs were monitored and although occasional increases in rate were observed (e.g. from 25 - 35 ventilations per min), there was no trend to indicate that ventilation rate had anything to do with any specific aspect of mating. At the termination of mating the females usually had the distinctive sucker marks left on their mantle.

It is noteworthy that in most mating observations the male was smaller than the female; therefore, some factor other than size was important in domination of mating activity. In the field observation of mating (Eleuthera Island, Bahamas) a female 85 mm ML was mated by a male 53 mm ML during mid-morning. This substantially smaller male completely dominated the entire sequence - swimming across the bottom, mounting the female and mating her for 58 mins. The remarkable facet of this mating is that only minutes before this was observed, the 85 mm ML female had been found under a sponge eating the remains of another male that was 53 mm ML (Hanlon, 1983). Therefore, the receptivity of females apparently can change within hours and could be associated with their state of hunger, the degree of aggressiveness of the male or perhaps some hormonal or pheromone factor.

No single body pattern was associated with mating. In several cases the male would be in a pattern in which the arms and web were in Uniform Light Phase and the head and mantle were uniformly dark brown. However, in most cases, both animals were either in Uniform Light Phase or Chronic General Mottle. In the field observation, the mating pair was initially in Uniform Darkening, but then gradually returned to Uniform Light Phase in which they were a light brown color.

In all but one of the 13 mating observations the animals did not seek cover or protection. Even in the field the octopuses mated during the day in the open part of the reef. This seems to be a very dangerous way to conduct an important part of the life cycle, but it remains to be proven whether all animals in nature mate during the day in the open. Mating with a larger female could be risky for a male *Octopus briareus.* The danger of being captured and eaten if she is non-receptive could be greater than the risk of being sighted by a passing predator. Thus it can be to the male's advantage to mate during the day in the open where he can more effectively monitor visually the receptivity of the female and have room to escape if necessary.

In one laboratory observation, the male remained within its den and extended his hectocotilized arm toward the female sitting motionless on top of a rock about 10 cm away. Copulation was observed for approximately 10 min, at which time the female flashed Uniform Darkening and reached for the male, who inked and fled.

In all observations of mating the animals were 200 to 250 days old, or in a size range of approximately 50 to 100 mm ML. This conforms generally to the time at which *Octopus briareus* is thought to become mature. The hectocotylus has been found in males as small as 27 mm ML. In laboratory reared males the earliest observation of the appearance of the hectocotylus was in four males between 40 and 50 mm ML (133 days old, 26 - 59 g). Available evidence indicates that females become mature at a similar size and age as males. Examination of females in the University of Miami Museum indicate that ripe ovaries are found in animals in the range of 35 to 81 mm ML, and females 45 to 120 mm ML have laid eggs. Conversely, females 18 to 45 mm mantle length are generally immature (Hanlon, 1983).

Sperm storage can be as long as 100 days before egg laying. Female behavior begins to change prior to egg laying: they reduce their food intake and they find or construct a suitably protected lair in which to lay the eggs. Females constantly guard and clean the eggs and can only be separated from them forcibly. The females appear not to forage for food, but will often eat during egg brooding by grabbing crabs that stray close to the lair.

Since males and females mate promiscuously, it is likely in nature that individual females receive sperm from several males. Sperm storage is thought to take place in the oviduct or the oviducal gland, and it would be interesting and informative to know if there is any form of sperm competiton and what effect it would have on the genetic makeup of the population.

Unusual behavior by the female was noted after one copulation. Five minutes after termination of mating the female inhaled, raised her mantle straight up for five to eight seconds, then exhaled forcibly while lowering the mantle to its normal position. Two minutes later, while sitting in the head-high position, she furiously curled her wriggling arms back and forth over the mantle for 30 secs and then continued this behavior every four minutes. In the interim she would place from one to three arms into her mantle cavity for approximately 20 secs then suddenly withdraw them with a contraction of the mantle. This behavior continued for seven hours and the ventilation rate remained high, from 38 to 42/min. Thereafter, her behavior was completely normal. This behavior remains enigmatic.

Females that have been mated will frequently die without laying eggs, despite producing a large number of eggs in the ovary. In a normal female, eggs constitute one-third of the mantle cavity, while in abnormal females the eggs constitute roughly two-thirds of the mantle cavity. In the latter case the internal organs are often compressed anteriorly into a small volume. Several dissected specimens showed that the proximal oviducal aperture was closed. Eggs pass via this aperture from the ovary to the proximal oviduct. The result is that eggs cannot be laid, and the eggs begin to decompose in the ovary. Presumably it is some artifact of the laboratory that results in this condition.

INTERSPECIFIC INTERACTIONS

FEEDING AND ATTACK BEHAVIOR: Three distinct feeding maneuvers were observed in the laboratory: Parachute Attack, Side Arm Attack, Pincer Feeding Approach. The Parachute Attack is illustrated in figures 23, 49, 50. Octopuses as young as 22 days began to use Parachute Attack and by 70 days it was a commonly used attack maneuver. The young animals would often miss the prey entirely by descending short of the prey. Head bobbing (Comp. 32) was first recorded at this time. The animals would bob their heads before the attack, presumably to aid in monocular paralax. A typical sequence of feeding would be as follows. As the crab is sighted, the octopus raises its head turning one eye toward the prey; respiration rate increases and the eye and head region or the entire body would darken. Head bobbing ensues as the octopus leans toward the prey. The arms would coil beneath the body in preparation for the attack. The octopus would then launch itself forward in the Parachute Attack sequence. Upon capturing the prey, the octopus goes to Uniform Darkening for approximately ten seconds before it reverts back to Acute Mottle and returns to its den to consume the prey.

The Side Arm Attack sequence was used to seize prey nearby. The closest three or four arms would be curled and rolled back, then rapidly extended outward and upward, seizing the prey and pulling in into the web. Uniform Darkening is associated with this maneuver. Newly hatched octopuses use some parts of this attack sequence, but the fully developed attack and its associated body pattern was not observed until 44 days posthatching.

The Pincer Feeding Approach (Fig. 45) was observed less often than the other two methods. The octopus faces the prey and, with the second arms extended forward and the first and third arms extended outward, would distend the mantle with water, cease respiratory movements and move forward by subtle movements of the suckers. Upon close approach, in a single motion arms II close the pincer while arms IV dart forward from underneath. Most commonly the Pincer Feeding Approach was used when one of the other two attack maneuvers failed. In any of the attack maneuvers, if the prey was lost sight of and had escaped, the octopuses would immediately go to exploratory behavior, extending the arms in all directions and investigating cracks and the undersides of rocks.

Octopus briareus would commonly attack, kill and eat many crabs in succession. With smaller prey, additional crabs were captured and held in the web until the first was killed and eaten, at which time the next would be moved to the beak, killed and consumed. In one demonstration, an adult octopus captured 50 crabs (*Uca* sp., 15 mm carapace width). This octopus completely consumed 40 crabs, nine were partially eaten and one escaped unharmed. A half-grown octopus, 40 mm ML, captured and consumed 17 *Uca* of the same size. Thus they have a large appetite.

The exact method of killing the prey is yet unknown. However, on numerous occasions crabs are seen to tremble violently from two to four minutes after they are held tightly near the buccal region of the octopus. The crabs were often held with their chelipeds towards the buccal mass, and in these animals no bite marks are found anywhere on the carapace. It is possible therefore that the toxin from the posterior salivary gland is released from the buccal area and absorbed directly through the gills of the crab. Bacq (1951) described a similar situation and Nixon (1984) has demonstrated that octopuses can externally digest the arthrodial membrane and the musculo-skeletal attachments of crabs without penetrating the exoskeleton. In other cases the crab is held near the buccal area in the reverse position and it is possible that the octoups is injecting the toxin through a small hole in the membranous joint of the carapace (Ghiretti, 1959). This issue requires further study.

REACTIONS TO PREDATORS AND NOXIOUS STIMULI: Table 5 is a summary of antipredatory adaptations of *Octopus briareus*. This table was constructed from laboratory and field observations, but some of the secondary and tertiary defenses are speculative. Like most cephalopods *O. briareus* spends the majority of its time concealed from predators. They are able to avoid attracting attention of most foraging predators with their malleable body form, their nocturnally active cycle and by remaining motionless against the substrate. Once detected by a predator, they either flee or use some form of flash behavior to make a predator hestitate in its attack sequence (all four acute patterns are used in this type of situation). All of these reactions have been observed in the laboratory when an experimenter moves a hand swiftly toward an octopus in its tank or creates a similar artificial disturbance.

Gruber (1973) observed the reactions of *Octopus briareus* to eels *(Gymnothorax moringa)* in the laboratory. In 249 trials he found the following order or reactions: no response, 148; Uniform Darkening with papillation, 51; flight response, 35; inking, 9; Protective posture, 6. His experimental apparatus was not natural and thus this order of occurrence can not be construed as the natural response reactions. However, they do give an idea of the types of reactions an octopus is likely to use. In one of our own experiments *O. briareus* showed the Deimatic pattern to a moray eel after it had bitten one of the arms off. In that trial the octopus then followed the Deimatic pattern with a large discharge of ink and no further attack occurred.

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THE ECOLOGY OF *OCTOPUS BRIAREUS* ROBSON IN A BAHAMIAN SALTWATER LAKE

RICHARD B. ARONSON
DEPARTMENT OF PALEOBIOLOGY
NATIONAL MUSEUM OF NATURAL HISTORY
SMITHSONIAN INSTITUTION
WASHINGTON, D. C. 20560, U. S. A.

ABSTRACT

This paper describes a dense population of *Octopus briareus* Robson living in Sweetings Pond, a saltwater lake on Eleuthera Island, Bahamas. The animals sheltered in cavities within or under discrete sponge, coral and bivalve formations, and these dens appeared to be limiting. In general, *O. briareus* occupied dens for periods on the order of days. They usually remained in their dens during the day, except for mating and occasional hunting, and foraged primarily at night. They preyed on bivalves, crabs, fishes, mysid shrimps, polychaetes and each other. Apart from cannibalism, there were no observations of predation on Sweetings Pond *O. briareus.*

Copulation was observed three times during the day, and was similar to the laboratory observations of other investigators. Females guarding eggs were observed year-round in Sweetings Pond, in contrast to the reproductive seasonality of *Octopus briareus* off southeastern Florida. Egg and clutch sizes, development times, the high hatching success (98.8%), and the mean size of brooding females were similar to previous findings for *O. briareus.* Most animals showed signs of injuries in the form of scars, or severed or regenerating arms. Animals suffered injuries in territorial and cannibalistic encounters, and during mating.

In contrast to Sweetings Pond, octopuses were rare off the west coast of Eleuthera. Predators, rather than dens, probably limit *Octopus* populations in coastal habitats. The high lake density was due in part to the reduction in number of predatory fishes. Data presented here form a basis for future comparisons with coastal *Octopus* populations.

Octopuses exploit a variety of benthic habitats, including rocky shores and coral reefs, where they face strong competition and predation pressure from fishes (Packard, 1972). Octopuses can be important predators themselves in these habitats (Fotheringham, 1974; Simenstad *et al.*, 1978; Fawcett, 1984), and they influence the behavior of certain marine invertebrates (Ross and Boletzky, 1979; Wells, 1980; Fawcett, 1984). Until recently, however, little was known about octopus ecology, due primarily to their cryptic lifestyle.

Yarnall (1969) observed *Octopus cyanea* Gray under seminatural conditions (in artificial ponds) and describes hunting behavior, daily activity cycles and a dominance hierarchy based upon size. The activity cycle of *O. vulgaris* Cuvier has been studied (Altman, 1967; Kayes, 1974; Mather, 1988) and this economically important species has been examined from a fisheries viewpoint (Hatanaka, 1979a,b; Guerra, 1981; Smale and Buchan, 1981). The ecology of *O. dofleini* (Wülker) is the subject of ongoing research in British Columbia (Hartwick *et al.*, 1978a, b, 1981, 1988; Hartwick and Thorarinsson, 1978), and ecological field studies of *O. joubini* Robson (Butterworth, 1982; Mather, 1982) and *O. bimaculatus* Verrill (Ambrose, 1982, 1988) have been carried out as well.

From 1980 to 1983, I examined the ecology of *Octopus briareus* Robson in Sweetings Pond, a saltwater lake in the Bahamas. The absence of predatory fishes in Sweetings Pond has resulted in a unique community, of which *O. briareus* is the top carnivore (Aronson and Harms, 1985; Aronson, 1986). Here I treat a variety of topics pertaining to *O. briareus* ecology and behavior and, where information is available, compare the results to previous octopus studies. Hopefully, this paper will serve as the basis for future comparison with octopus populations in coastal habitats.

STUDY AREAS

Sweetings Pond is situated at the north end of Eleuthera Island, Bahamas (25°21′N, 76°30′W; Fig. 1). It is surrounded by karstic limestone and has surface area of

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0.92 km². The maximum depth is 15.3 m. Unconsolidated sediment covers a limestone pavement forming the bottom of the lake. The water chemistry and tidal cycle of Sweetings Pond indicate a connection to the west coast of Eleuthera via one or more restricted subterranean passages and/or percolation through the porous rock (Aronson, 1985). Human activity is negligible.

Figure 2 illustrates the marked benthic zonation observed in the area of the Cove Entry (Fig. 1) in 1980. From shore to a depth of approximately 2 m, thick, fluffy mats of the filamentous green alga *Cladophora crystallina* (Roth) dominated the substratum. Between 2 and 8 m depth, sponge, coral and bivalve formations (Table 1) were scattered over the bottom. These structures either rested atop the sediment or were loosely buried. Because of the discrete nature of the formations, this zone was termed the "patch zone." The main concentration of *Octopus briareus* occurred in cavities in and under some types of patch zone formations. Other octopuses were found under limestone rocks at shore. The patch zone thinned at its deep end, being composed mostly of flat orange sponges at a depth of 7.5 m. From the end of the patch zone to the center of the lake, the bottom consisted mainly of bare sediment, with scattered clumps of algae.

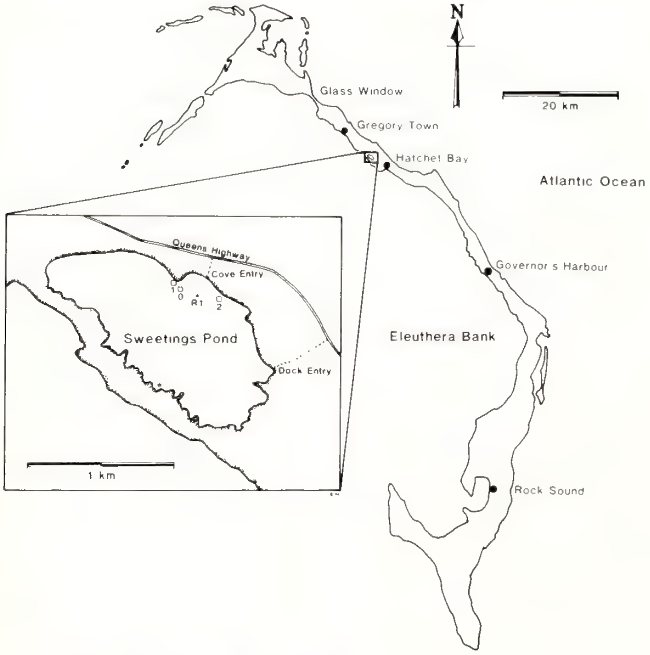

Fig. 1. Map of Eleuthera Island, Bahamas, showing location of Sweetings Pond. Inset: map of Sweetings Pond, showing locations of Study Plots (numbered squares). R1 is the survey, collecting and experimental area. Dashed lines are dirt tracks. Adapted with permission from Bahamas Department of Lands and Surveys maps.

Notable in the patch zone was the high density of ophiuroids, particularly the epifaunal suspension-feeder *Ophiothrix oerstedi* Lütken, which occurred at densities up to 434 ind./m² (Aronson and Harms, 1985). Other conspicuous mobile invertebrates were the large spider crab *Mithrax spinosissimus* (Lamarck), the starfish *Echinaster sentus* (Say), the sea urchin *Echinometra viridis* Agassiz, the polychaete *Eunice rubra* Grube and the gastropod *Fasciolaria tulipa* (Linnaeus).

In 1982 and 1983, much of Sweetings Pond did not follow the generalized profile of figure 2. Considerable areas were overgrown by *Cladophora* mats, and these mats expanded and regressed during 17 months of study. The cove that contains the Dock Entry (Fig. 1) was entirely patch zone in 1980. In February, 1983, almost the whole cove was covered by *Cladophora*, but the mats were dying back by June, 1983. Off the Cove Entry, a major portion of patch zone was covered by algal mat in 1982 to 1983. The algae destroyed all patch zone formations, leaving bleached coral skeletons and empty shells of *Chione cancellata* (Linnaeus) (the most common infaunal bivalve) and *Arca imbricata* Brugière after it regressed. In this way much *Octopus* habitat was destroyed, including Study Plot 1 (Fig. 1). The cause of these dramatic changes in algal cover is unclear, but nutrient input via runoff from the cultivated fields surrounding Sweetings Pond could be responsible.

The fish fauna of Sweetings Pond was remarkably depauperate: 17 species from 15 families were recorded (Aronson and Harms, 1985). By contrast, 126 species from 50 families were recorded in shallow water (≤ 6 m depth) off the west coast of Eleuthera in the vicinity of Sweetings Pond. The only potential predators of *Octopus* sighted in hundreds of hours of diving in the lake were five schoolmasters, *Lutjanus apodus* (Walbaum), one Nassau grouper, *Epinephelus striatus* (Bloch), and one moray eel, *Gymnothorax funebris* Ranzani (see Randall, 1967).

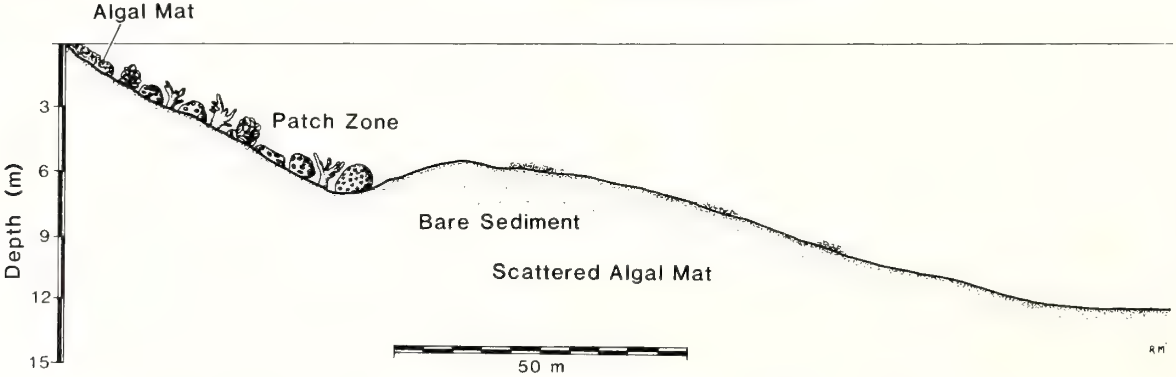

Fig. 2. Benthic profile from the Cove Entry to the center of Sweetings Pond in July, 1980.

Table 1. Principal formations in the patch zone of Sweetings Pond. Combinations of these types were also encountered.

TAXA	ASSIGNED NAME	REMARKS
A. Sponges		
Xestospongia sp.	brown sponge	often with *Arca* attached
Halicometes sp.	orange sponge #1	
Suberites sp.	orange sponge #2	
Reniera sp.	white sponge	
B. Coral-dominated		
Porites porites (Pallas) *Arca imbricata* Brugière	*P. porites*-bivalves	
Porites astreoides Lamarck		large head with scattered *Arca*
Siderastrea spp.		small heads; rare
C. Bivalve-dominated		
Arca imbricata *Chama macerophylla* (Gmelin) *Lima scabra* var. *tenera* (Sowerby) *Pinctada imcricata* Röding	bivalve clump	chiefly *Arca* and *Chama*

METHODS

Ecological information was collected in 1980 and 1982-83 during approximately 450 SCUBA and snorkel dives from the shore of Sweetings Pond. For comparison, more than 150 day and night dives were made off the west coast of Eleuthera between Governor's Harbour and the Glass Window (Fig. 1).

The discrete nature of the patch zone formations facilitated mapping, and their lack of strong attachment to the substrata allowed them to be turned over carefully and then replaced. In July 1980, three surveys were conducted in a 30x30 m area of the patch zone (Study Plot 0; Fig. 1), gridded with nylon line to form squares 3 m on a side. The surveys involved examining each formation in the plot for *Octopus briareus*. When an individual was found, it was captured, measured, and sexed; and the formation position, type, size, and depth were recorded. The animal was then returned to its den. In addition, numerous census dives were made in the patch zone to the southeast of the Cove Entry. Two divers swam zig-zag patterns through the entire depth range of the patch zone and captured each animal encountered. The same ecological information was taken as in the surveys of Study Plot 0, but the position of the formation was not mapped.

Two 27x30 m grids (Study Plots 1 and 2), with the same element size as Study Plot 0, were constructed in the patch zone in April 1982. These were surveyed monthly. Study Plot 1 was not surveyed after July 1982 because it became almost completely overgrown with *Cladophora*, whereas Study Plot 2 was surveyed through July 1983. Monthly patch zone survey dives were also made off the Cove Entry and southeast, near Study Plot 2. These dives were made as close in time as possible (usually on the same day) to the Study Plot surveys, to minimize the possibility of encountering individual *Octopus briareus* twice. The divers' search procedures were the same as for the census dives of July 1980.

All research on den ecology was carried out between the hours of 0800 and 1300 EST. During this time interval, 96% (457/476) of the *Octopus briareus* encountered in Sweetings Pond under natural conditions were in dens (see Diel Activity Pattern). Dives were made at all hours of the day and night to observe diel activity patterns, feeding habits and reproductive behavior.

For convenience, the word "dorsal" will be used to refer to the upper surface of the octopus when it is resting on the bottom or swimming in its usual orientation. The designation "ventral" will be in keeping with the above definition. This simplification follows Wells' (1978) suggestion.

RESULTS AND DISCUSSION

DENSITY, SPATIAL DISTRIBUTION AND DEN ECOLOGY

Octopus briareus occurred at high density in Sweetings Pond. In July 1980 the three surveys of Study Plot 0 (900 m^2) yielded counts of 11, 14 and 16 individuals (mean 15.3 ± 3.1 SD ind./1000 m^2). Density varied from area to area of the patch zone, apparently depending on the availability of suitable dens (see below). In April, 1982, for example, Study Plots 1 and 2 (810 m^2) were surveyed and found to contain 12.3 ± 1.2 SD and 4.1 ± 1.5 SD ind./1000 m^2, respectively (n = 3 surveys). The 1982-83 mean for Study Plot 2 was 7.9 ± 3.6 SD ind./1000 m^2 (Aronson, 1986).

A nearest neighbor analysis (Clark and Evans, 1954; Poole, 1974) was performed on the spatial distribution of *Octopus briareus* in the three surveys of Study Plot 0. There was no significant deviation of mean nearest neighbor distance from that expected had the animals been dispersed randomly. The same analysis was performed for four categories of dens potentially occupied by *O. briareus:* brown sponges showed significant clumping ($p<0.005$), *Porites porites*-bivalve clumps were evenly dispersed ($p<0.0005$), and bivalve clumps and orange sponges were distributed randomly ($p>0.40$).

While it was impossible to predict whether a particular formation was suitable as a den, some formations were occupied frequently while others remained unoccupied (Fig. 3;

see also Aronson, 1986 for statistical analysis). The implication is that dens could be the limiting resource for *O. briareus* in Sweetings Pond. This hypothesis is supported by experiments in which local density was increased substantially by adding artificial dens to patch zone plots (Aronson, 1986).

Mather (1982) found that the distribution of *Octopus joubini* in a Florida soft-bottom community correlated with the availability of dens. Ambrose (1982), on the other hand, concluded that suitable dens were not limiting to *O. bimaculatus* on hard substrata off Santa Catalina Island, California. In a removal experiment, Hartwick *et al.* (1978a) found that some dens were occupied by *O. dofleini* of similar size to the previously evicted occupants; however, dens were not limiting in the rocky subtidal off Vancouver Island, British Columbia (Hartwick *et al.*, 1988). On the other hand, cavities may have been limiting in offshore, soft-bottom habitats (Hartwick *et al.*, 1988). Adding artificial dens to an octopus fishing ground off Japan increased the catch dramatically, implying that dens were limiting there (Tauchi and Matsumoto, *fide* Mottet, 1975). Ambrose (1982) suggests that dens are more likely to be limiting in soft-bottom communities like Sweetings Pond. In general, rocky subtidal habitats contain more crevices, but how cavity-occupying fishes and invertebrates affect the availability of dens is unknown (Aronson, 1986).

Hartwick *et al.* (1978a) found that the *Octopus dofleini* in their study were more evenly spaced than expected in a random distribution. This result, combined with an observation of intraspecific fighting over a den (Kyte and Courtenay, 1977), helps make the case for the commonly held view that *O. dofleini* is territorial (Hartwick *et al.*, 1978a). Woods (1965) and Cousteau and Diolé (1973) present anecdotal evidence for territoriality in natural populations of *O. vulgaris*; however, Altman (1967) and Kayes (1974) found no evidence of territorial behavior in this species. At Kayes' (1974) field site off Malta, dens "were found wherever the substrate was suitable, and occasionally occupied holes were only 1 m apart." Guerra

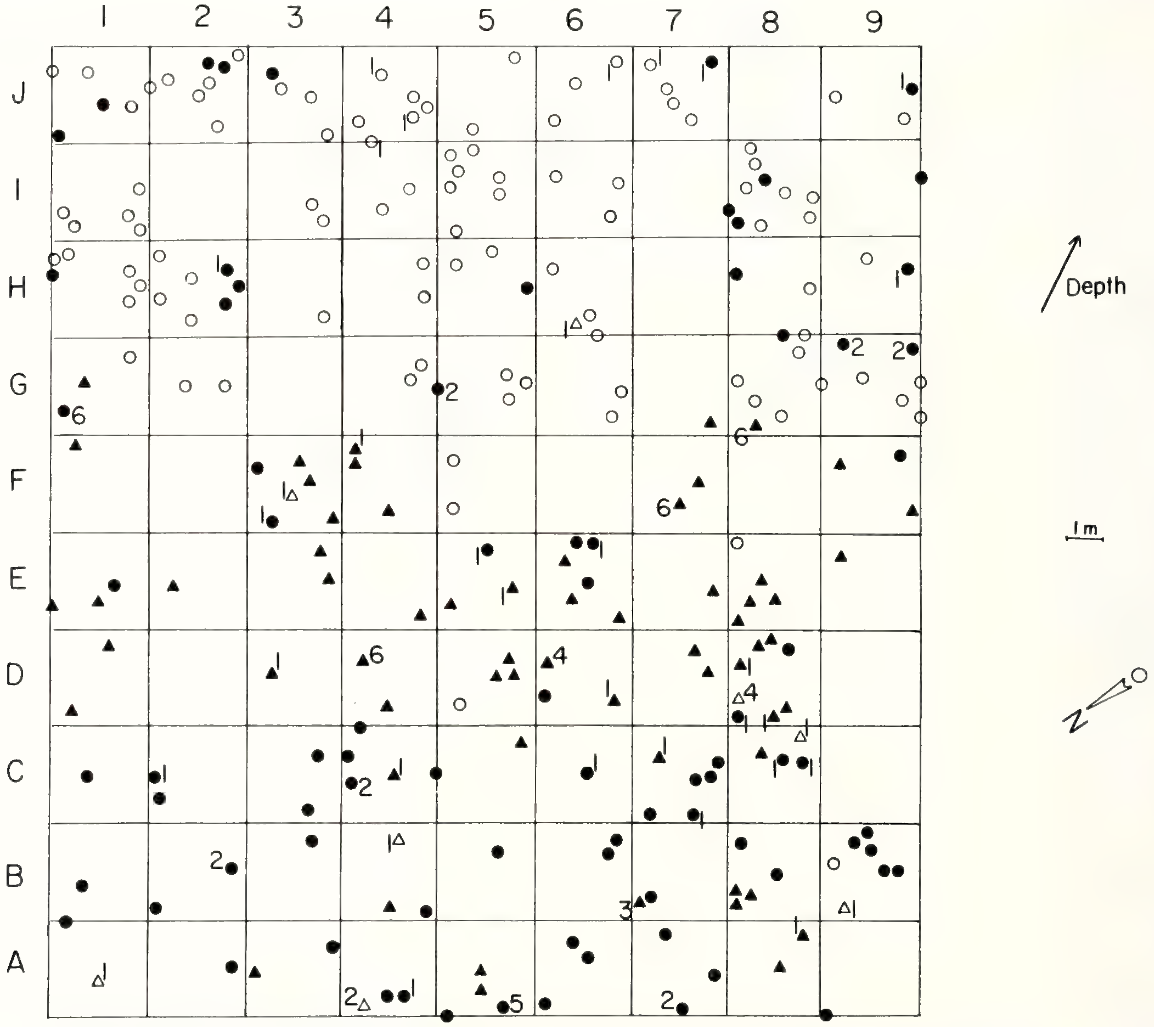

Fig. 3. Map of Study Plot 2, showing locations of *Octopus briareus* dens mapped during 1982-83. The number next to a formation is the number of different *O. briareus* that were found in or under the formation. Solid triangle, *Porites astreoides*; solid circle, brown sponge; open circle, orange sponge; solid square, mixed clump of *P. porites* and bivalves; open square, bivalve clump; open triangle, other. Formation types that were never occupied are not mapped, and the only "other" formations mapped are those that contained *O. briareus.*

(1981) concluded that *O. vulgaris* off west Africa were dispersed randomly within patches, the patches being of varying density. The minimum nearest neighbor distance observed under natural conditions in the present study was 80 cm, for a female and a juvenile inhabiting brown sponges. In artificial den experiments, *O. briareus* pairs of the same and opposite sexes occupied polyvinyl chloride (PVC) tubes as close as 15 cm (Aronson, 1986). Considering the spacing of natural dens seen in the Study Plots (Fig. 3), den defense probably did not affect nearest neighbor distance. Suitable dens were simply too far apart.

TENURE OF DEN OCCUPATION

The maximum tenure of den occupation in Sweetings Pond (based on daily den checks in the morning) was ≥ 25 days for animals not brooding eggs. This number is derived from observations of a female (mantle length 8.0 cm) that occupied the cavity under a brown sponge, disappearing after 25 days of observation. She had a swollen gonad and was apparently about to lay eggs, which could account for the length of her stay. Incidental observations of *Octopus briareus* denning under limestone rubble along the shore just off the Cove Entry gave a tenure of occupation on the order of a few days. Artificial dens (PVC tubes; Aronson, 1986) were also occupied for one to a few days, with a maximum of seven days (n = 81 observations).

The 1982-83 monthly surveys support these results. Eighty-five of 93 *Octopus briareus* were not found in the same den the previous month. Of the eight remaining, three were egg-brooding females seen in two consecutive months, one was an adult male seen in two consecutive months (recognized by injuries) and four were ambiguous cases (they might have been the same animals as in the previous monthly survey). The male was found twice in the same den 35 days apart.

Altman (1967) states that *Octopus vulgaris* were found in "permanent" or "temporary" homes in the field. "Permanent" homes were occupied for at least two consecutive days; of 37 dens observed, four were occupied for the duration of the study (25 days). Unfortunately, no information is given on the sexual state of these animals. Most *O. vulgaris* occupied dens for one to two days in Kayes' (1974) field study. Yarnall (1969) reported a maximum tenure of den occupation of 23 days for *O. cyanea* in artificial ponds and Van Heukelem (1966) reported a maximum occupancy of 35 days in the field (Hawaii). Most *O. dofleini* in the study by Hartwick *et al.* (1984) were found in the same dens for at least one month. Their results "indicate a pattern of large-scale movement interspersed with periods of residence in a relatively small area..." By far the longest periods of occupation observed are for *O. bimaculatus.* Almost half the population examined by Ambrose (1982) occupied the same dens for more than one month, and three individuals remained in the same dens for more than five months. *O. briareus* appears to be a fairly mobile species, both in Sweetings Pond and in coral reef habitats (Hochberg and Couch, 1971; J. Wodinsky, pers. comm.).

DEN BLOCKING AND EXCAVATION

Octopus briareus frequently blocked the entrances to their dens with small pieces of bivalve clump (mostly *Arca imbricata*), empty bivalve shells, pieces of live or dead *Porites porites* and live *Chione cancellata.* Such acitivity was most obvious when the animals resided in PVC or acrylic tubes but was sometimes unambiguously the case with natural dens as well. Blocking is a well-known behavior in *O. vulgaris* (Legac, 1969; Cousteau and Diolé, 1973) and also occurs in other species (Van Heukelem, 1966). The separate topic of middens outside octopus dens will be considered in Diet.

Den excavation has been reported in the literature for a number of species (Yarnall, 1969 for *Octopus cyanea*; Hochberg and Couch, 1971 for *O. macropus* Risso; Cousteau and Diolé, 1973 for *O. vulgaris*; Hartwick *et al.*, 1978a for *O. dofleini*; Ambrose, 1982 for *O. bimaculatus*). Excavation by funnel blasts from *O. briareus* was observed once in Sweetings Pond, and excavations under patch zone formations were in many cases obvious because of the different color of the sand that had been exposed.

DIEL ACTIVITY PATTERN

Hochberg and Couch (1971) characterize *Octopus briareus* as a nocturnal hunter, based on field observations in the United States Virgin Islands. Hanlon's (1975) field observations from a number of Caribbean localities support their conclusion. Ninety-six percent of *O. briareus* (n = 476) in Sweetings Pond were found in dens during the morning (0800-1300 hours EST). By contrast, 94% (n = 35) of individuals at night were out in the patch zone ($\chi^2=290.80$, df=1, $p<0.005$). Of these, four were sitting atop formations (their dens?) and 29 were moving along the substratum. Three out of 20 animals captured at night had prey (see Diet), although one individual captured during the day was carrying two small spider crabs, *Pitho* sp. (undescribed). The three observed instances of copulation occurred during the day (see Reproduction: Mating Behavior).

Different activity cycles have been reported for different *Octopus* species. *Octopus vulgaris* makes long excursions at night and early in the morning, with short trips during the day (Altman, 1967; Kayes, 1974; see also Mather, 1988). Altman (1967) raises the possibility that the activity pattern of *O. vulgaris* is related to those of prey or predator species. The prey activity hypothesis could also apply to *O. briareus* in Sweetings Pond: the bivalve *Laevicardium laevigatum* (Linnaeus) comes out of the sediment at night (see Diet). *O. joubini* is nocturnal (Mather, 1982, 1984), whereas *O. dofleini* showed only a slight activity peak at night in a sonic tagging study (Mather *et al.*, 1985). Houck (1982) demonstrated that three sympatric *Octopus* species in Hawaii displayed differences in diel activity cycles, possibly reducing competition or predation on smaller *Octopus* species by larger ones. The isolated population of *O. briareus* in Sweetings Pond would be ideal for comparison with coastal populations in a study of behavioral character displacement.

DIET

Information on the feeding habits of *Octopus* spp. has been derived primarily from the examination of piles of prey remains, or middens, that the animals leave outside their dens

(Van Heukelem, 1966; Altman, 1967; Hochberg and Couch, 1971; Kayes, 1974; Hartwick *et al.*, 1981; Smale and Buchan, 1981; Ambrose and Nelson, 1983). Obviously, such middens only preserve information on prey items that have hard parts and that are consumed in the den (Smale and Buchan, 1981). Furthermore, prey discards can disappear from middens due to biotic (hermit crabs) or abiotic (currents and surge) taphonomic processes (Ambrose, 1983). Middens have revealed that crustaceans and mollusks are important constituents of the diet of octopuses, but the information loss associated with middens argues against their use in quantitative analyses.

Octopus briareus middens were uncommon in the patch zone of Sweetings Pond, possibly, as Wolterding (1971) suggests, because of the high mobility of this species. At shore just off the Cove Entry, a number of middens were found outside occupied dens. Collections revealed the following prey species: the bivalves *Laevicardium laevigatum, Brachydontes domingensis* (Lamarck) and *Chione cancellata*, and the crab, *Pitho.* This species list is based on fresh discards (i.e. no signs of pitting or algal growth on them). The bivalves *Lima scabra* var. *tenera, Pinctada imbricata, Codakia orbiculata* (Montagu), *Polymesoda maritima* (d'Orbigny) and *Chama macerophylla* were also found in middens and in dens, but it was difficult to determine the freshness of these shells. *C. cancellata*, the most common infaunal bivalve in Sweetings Pond, presents a problem. Empty valves of this species are used for blocking by *O. briareus*, as are living individuals. *O. briareus* did not eat bivalves in a laboratory study (Wolterding, 1971).

An *Octopus briareus* captured during the day was carrying two *Pitho* sp. and an octopus encountered during a night dive held a mysid shrimp. *O. briareus* also eat fishes and polychaetes (Hochberg and Couch, 1971; Wolterding, 1971; Hanlon, 1975). One octopus, captured at night, was eating the fish *Callionymus pauciradiatus* Gill, and another examined at night was holding an unidentified polychaete. On two occasions, *O. briareus* found in their patch zone dens during the day were eating polychaetes, *Eunice rubra.*

Cannibalism is known in field populations of *Octopus vulgaris* (Smale and Buchan, 1981), *O. dofleini* (Hartwick *et al.*, 1978a) and *O. bimaculatus* (Ambrose, 1984), and this behavior is well documented for a variety of species kept in aquaria (e.g. Lane, 1974). Wolterding (1971) and Hanlon and Forsythe (1985) observed cannibalism by *O. briareus* in the laboratory, and Hanlon (1983) discusses some of the instances observed in the present study. Six observations of cannibalism were made in Sweetings Pond in 1982-83 (Table 2). In the observation of 13 July 1982, the female copulated a few minutes after she was discovered eating a different male. Direct observations and examination of crop contents revealed that the arms are eaten first. One victim (17 July 1982) had had all of its arms eaten yet was still alive. When removed from the grasp of the cannibalizing female, it made weak attempts to swim and crawl away. The potential interacton between cannibalistic and mating motivational states is discussed in the next section.

Table 2. Instances of cannibalism by *Octopus briareus* in Sweetings Pond. All observations are from 1982 (?, sex indeterminable in the field; —, no data).

	CANNIBAL		PREY	
Date	Mantle Length (cm)	Sex	Mantle Length (cm)	Sex
13 Apr	4.3	M	1.8	F
17 Apr	3.0	?	2.0	M
11 May	7.0	F	—	—
13 July	8.5	F	5.3	M
17 July	7.0	F	5.5	—
19 Aug	5.5	M	2.8	F

REPRODUCTION: MATING BEHAVIOR

Three copulations were observed. One occurred in July 1982 and is discussed by Hanlon (1983). This mating involved a 5.3 cm mantle length male and an 8.5 cm female, and lasted approximately 60 min. The second copulation, in August 1982, involved a 6.0 cm male and a 7.0 cm female. The female had been in an artificial den placed in the patch zone at 3.7 m depth. This den consisted of a length of 10 cm diameter acrylic tubing with a 5 cm entrance. The male was hiding under sandbags that covered the den. I removed the sandbags and evicted the female, at which point the male instantly leapt upon her dorsal mantle and they copulated. Mating lasted 67 minutes. At the end of copulation, the male dismounted abruptly and swam away (the male in the first copulation did not leave as quickly). The female was left with about 40 circular sucker scars on the posterior end of her dorsal mantle. The third instance was observed briefly in January 1983, but extensive observations were not possible (C. A. Harms, pers. comm.).

In all cases, mating was similar to laboratory observations (Wolterding, 1971; Hanlon, 1975) and occurred during the day. Noteworthy is the abruptness with which the male left the female in the second case. Females could attempt to cannibalize males after mating. In the first case, mating occurred just after the female had cannibalized a male (Hanlon, 1983). By retreating hastily, the male in the second copulation could have been avoiding capture by the female; in fact, he was already missing all of his third left and part of his first right arms. As mentioned in Injuries, the only causes of arm loss in Sweetings Pond appear to be intraspecific fighting and cannibalism.

The absence of precopulatory behavior in *Octopus briareus* under laboratory and field conditions (Hanlon, 1983 and references therein; this study) is in marked contrast to the ritualization seen in *O. cyanea* (Van Heukelem, 1970; Wells and Wells, 1972). Male *O. vulgaris* perform a "sucker display" when initiating mating with a larger female (Packard, 1961). It could be that the pattern of physical contact itself (i.e. the male's climbing on top of the female's mantle) serves to identify the *Octopus* male to the female (Wells and Wells, 1972). Considering the variation in copulatory behavior reported in *O. cyanea* and *O. vulgaris* (Wells and Wells, 1972; Wodinsky, 1973; also see Mather 1978 on *O. joubini*), including instances in which the males of these species also leapt upon the females, the apparent simplicity of mating initiation in *O.*

briareus merits further attention.

REPRODUCTION: EGGS AND EGG BROODING

In censuses from March 1982 to July 1983, females guarding eggs were recorded in Sweetings Pond in each month except June and July 1983, with annual peaks in February and March (Aronson, 1986). In southeastern Florida, *Octopus briareus* seem to display a more strongly seasonal maturation and breeding cycle (Hanlon, 1983); the degree of synchrony may therefore vary from population to population.

The mean egg length, computed from eggs at development Stage IV (Wells and Wells, 1977) or earlier was 10.50 ± 0.68 SD mm (range 9.0 - 12.0 mm, n = 99; based on 11 eggs each from nine females). The mean mantle length of females guarding eggs was 6.1 ± 0.92 SD cm (n = 25). Two egg broods, followed from stage IV or earlier to hatching, gave a development time range of 50-67 days. The first female brooded her eggs for 50 days (11 May-30 June 1982; 23.5-32.0°C) and the second for 67 days (18 January-26 March 1983; 20.5-23.5°C). The value of 36 days quoted by Hanlon (1983) for development time in Sweetings Pond was an early minimum estimate.

Clutch sizes were determined from egg strands collected within two days of hatching. For each egg strand, the number of empty attached capsules and the number of egg stalks from which the capsule had been separated were counted. This procedure avoided the destruction of clutches, which would have been necessary had the eggs been counted prior to hatching. The error caused by possible loss of hatched strands was minimal. The mean clutch size was 267.3 ± 99.2 SD eggs (range 97 - 414 eggs; n = 8). There was no correlation between clutch size and the mantle length of the brooding female (product-moment correlation coefficient, r = −0.20, n = 8, p > 0.90; Sokal and Rohlf, 1969). Hatching success was high: 1453 of 1471 eggs (from 6 females) hatched, for a success rate of 98.8%. The egg sizes, clutch sizes, development times, hatching success and average size of brooding females were similar to previous findings for *Octopus briareus* (Hanlon, 1983).

INJURIES

Two classes of injury were noted for *Octopus briareus* in Sweetings Pond: arm injuries and scars. Arm injuries consisted of severed or regenerating arms. Arm injuries can result from cannibalism, and *O. briareus* can also lose or autotomize (Lange, 1920) arms in fights. In a fight staged by divers between a female of mantle length 4.0 cm and an 8.0 cm female, the smaller one lost three arms. However, neither octopus lost any arms in the only fight observed under natural conditions. In this case two males, 4.5 and 5.5 cm in mantle length, were struggling underneath a brown sponge. The larger individual clearly had the advantage in both fights. It was impossible to tell whether these were territorial or predator-prey encounters, or both.

Scars occurred in a number of forms (Fig. 4). They were usually on the head, or dorsal or ventral mantle, although they occurred on the arms as well. Many scars were rings. In other cases, white lesions of varying sizes appeared on the mantle, arms or webbing where patches of skin had been removed. Still other scars were dark or light lines.

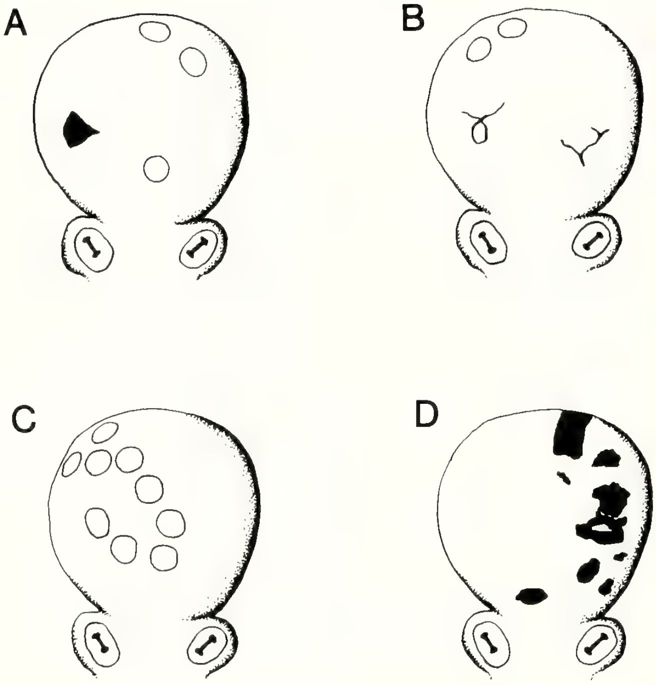

Fig. 4. Sample of *Octopus briareus* dorsal mantle scar patterns. All scars are drawn in negative. A, sucker marks and a triangular skin lesion; B, sucker marks and lines; C, sucker marks, perhaps from a single *O. briareus* arm; D, extensive skin lesions.

From the second observation of copulation, it is obvious that the dark ring scars were sucker marks. Skin lesions could arise from the suckers or beak bites of other octopuses; they could also result from infections or from scraping against rough surfaces. Linear scars, rarer than the other two categories, are of unknown origin. Scars can be acquired during mating, in encounters with cannibals and during fights.

There was no evidence of injuries caused by interspecific interactions (in contrast to Hartwick *et al.*, 1988). The only animals common enough and large enough to have posed a threat to *Octopus briareus* were spider crabs, *Mithrax spinosissimus*, which reached at least 20 cm in carapace width. However, these herbivorous crabs became quite alarmed and retreated when *O. briareus* were placed near them.

Larger *Octopus briareus* displayed the results of injuries more frequently than did smaller ones (Table 3). The most obvious explanation is that the probability of an older individual having interacted with a conspecific is greater. Males and females not guarding eggs showed about the same frequency of injury. Females guarding eggs showed a high rate of arm loss and scarring, possibly due to cannibalism by copulating males and the effects of their suckers, and to the general deterioration associated with egg-brooding. It would be interesting to see whether *O. briareus* in low-density coastal populations, which presumably encounter conspecifics less

Table 3. Breakdown of injuries for *Octopus briareus* in all 1982-83 surveys combined. "Unsexable" individuals were those ≤4.0 cm mantle length.

A. Scars

Sex category	Number of animals (proportion) With injury	 Without injury	N
Males	79 (0.73)	29 (0.27)	108
Females (no eggs)	62 (0.77)	19 (0.23)	81
Females guarding eggs	14 (1.0)	0 (0)	14
Unsexed Adults	4 (1.0)	0 (0)	4
Unsexable	10 (0.12)	73 (0.88)	83

B. Severed or regenerating arms, or parts of arms

Sex category	Number of animals (proportion) Missing arm or part	 Missing only tip(s)[a]	 Without injury	N
Males	11 (0.10)	9 (0.08)	89 (0.82)	109
Females (no eggs)	11 (0.13)	0 (0)	73 (0.87)	84
Females guarding eggs	6 (0.55)	0 (0)	5 (0.45)	11
Unsexed Adults	5 (1.0)	0 (0)	0 (0)	5
Unsexable	2 (0.02)	1 (0.01)	85 (0.97)	88

[a]The distal centimeter or less of the arm.

often, show lower injury frequencies.

It was possible to identify individual animals by a combination of size (good on a short-term basis), sex, mantle scar pattern, and arm injury/regeneration pattern. Individual identifications were used in mapping the occupants of Study Plot 2 and in determining the tenure of den occupation. The scar patterns were very distinctive, and although widely divergent scar patterns were chosen for figure 4, far more subtle distinctions could be made. Cephalopod arms take on the order of months to regenerate (Lange, 1920; Féral, 1978). While this is not as sure an identification technique as branding (Van Heukelem, 1973) or subcutaneous dye injection (Altman, 1967; Hochberg and Couch, 1971; Kayes, 1974), it eliminates the trauma of those procedures. To compensate for the possible loss in accuracy of animal identification, ambiguous cases were always rejected as data. The technique obviously worked better for larger than for smaller animals.

OCTOPODS OFF THE COAST OF ELEUTHERA ISLAND

Octopus briareus occurred in and around subtidal crevices along the rocky west coast of Eleuthera. Compared to the density in Sweetings Pond, *Octopus* spp. were rare off the west coast. In 1982 and 1983, *Octopus* were seen four times in shallow diving (<5 m) at sites from Governor's Harbour to the Glass Window. One *O. macropus* was seen at night, two *O. briareus* were observed, one at night and one in the afternoon, and an *Octopus* sp. (probably *briareus*) was seen in the evening. While it is true that many cavities in the limestone rock were too deep to be searched effectively, 166 day and night dives were made specifically to search for octopuses. Dens did not appear to be limiting off the west coast (Aronson, 1986).

GENERAL DISCUSSION AND CONCLUSIONS

The population of *Octopus briareus* in Sweetings Pond has persisted from at least 1972 to 1988 (pers. obs.). How the species was introduced to this "island" is undetermined. Perhaps introduction occurred from the west coast of Eleuthera through subterranean passages.

Island populations are often subject to less predation pressure than they experience on the "mainland", resulting in high densities (MacArthur and Wilson, 1967). Release from predation probably accounts for the high density of *Octopus briareus* in Sweetings Pond. Of the 29 species of Caribbean reef fishes listed by Randall (1967) as eating cephalopods, only two (*Epinephelus striatus* and *Lutjanus apodus*) were observed in Sweetings Pond, and these were rare. A single moray eel, *Gymnothorax funebris*, was sighted in the lake. By contrast, 19 of Randall's (1967) cephalopod predators occur off the west coast of Eleuthera and I suspect that predatory fishes limit *Octopus* populations there. The low abundance and diversity of predatory fishes in Sweetings Pond could be due to chance factors associated with colonization, or the lake could be too small to sustain populations of top-level carnivores (MacArthur and Wilson, 1967). Hamner (1982) has anecdotally reported similar island effects for the faunas of the Palau salt lakes.

In a soft-bottom habitat such as Sweetings Pond, it is not surprising that dens were limiting to a high-density *Octopus briareus* population. Predation is probably more important than den availability in limiting Bahamian coastal *Octopus* populations. The ethological consequences of this ecological difference are as yet unknown. Whether predators of *O. briareus* exert a limiting influence at the recruitment and juvenile stages (Ambrose, 1988) or by preying on adults is also not known.

I have argued elsewhere (Aronson and Harms, 1985; Aronson and Sues, 1987) that Sweetings Pond, which is dominated by an epifaunal, suspension-feeding echinoderm (the ophiuroid *Ophiothrix oerstedi*) and a predatory cephalopod, can be viewed as a modern-day analogue of certain Paleozoic and Early Mesozoic soft-bottom communities. The exclusion of predatory reef fishes is apparently responsible for the high density of both species in the lake. Ancient epifaunal, suspension-feeding communities, populated by carnivorous ectocochliate cephalopods, could also have persisted due to low predation pressure from fishes (Aronson and Sues, 1987). Comparing a dense, isolated *Octopus briareus* population, and the fauna of Sweetings Pond as a whole, to coastal populations could provide clues to the structure of ancient benthic marine communities.

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AN ATLANTIC MOLLUSCAN ASSEMBLAGE DOMINATED BY TWO SPECIES OF *CRASSINELLA* (BIVALVIA: CRASSATELLIDAE)

WILLIAM G. LYONS
FLORIDA DEPARTMENT OF NATURAL RESOURCES
ST. PETERSBURG, FLORIDA 33701, U. S. A.

ABSTRACT

A total of 136 molluscan species were obtained in benthic grab samples during 12 bimonthly periods (Sept 1971 - July 1973) at five stations (depths 7-11 m) near Hutchinson Island, east central Florida; 33 characteristic species constituted 90% of the 4135 specimens. Species distributions were influenced strongly by sediment composition. Compacted fine and very fine sands of the beach terrace supported few mollusks. Well-sorted medium sands supported a small but abundant species group at an offshore shoal, and two larger species groups were associated with coarse sands and with large shell particles that entrapped mud and silt in a trough between the shoal and terrace. Two bivalve species were numerically dominant. *Crassinella lunulata* (Conrad, 1834) contributed 33% of all specimens and occurred among large shell particles in the trough; *C. dupliniana* (Dall, 1903) contributed 14% of all specimens and favored medium sands at the shoal. *C. dupliniana*, originally described as a fossil, has not been recorded previously among living fauna.

Only two studies have examined the species composition and relative abundance of small mollusks associated with microhabitats of the continental shelf of the southeastern United States. Both studies addressed assemblages dominated by corals (McCloskey, 1970; Reed and Mikkelsen, 1987), so, expectedly, most of the mollusks were species with affinity for hard substrata. Consequently, very little is known about species associated with various sediment regimes of the shelf.

Opportunity to acquire information on sand-bottom species associations on the inner continental shelf of eastern central Florida occurred during 1971 through 1973, when the Florida Department of Natural Resources (FDNR) conducted a study to assess potential environmental impacts from a nuclear power plant then under construction at Hutchinson Island. Offshore environments were sampled with trawls, plankton nets, and benthic grabs; the surf zone was sampled with beach seines; and specimens were collected by hand from a rocky shore community. Several technical reports on environmental parameters, species composition, distribution, and seasonal fluctuations of biota from those samples have been published in *Florida Marine Research Publications.*

Two species of the bivalve genus *Crassinella* were numerically dominant among mollusks in quantitative grab samples obtained off Hutchinson Island. Associations of those species with other small infaunal-epifaunal mollusks and the relationship of those associations to different sediment regimes are reported here. One of the species, not recognized previously in Recent fauna, is illustrated and compared with congeners.

METHODS

Five benthic stations on the nearshore continental shelf (Table 1, Fig. 1) were sampled bimonthly for two years (Sept 1971 - July 1973). A Shipek benthic grab was used to obtain five replicate samples at each station during each visit; each grab sampled 0.04 m^2 of bottom surface area. Station sediments were sieved, described, and classified to type during 8 of the 12 sampling periods (Sept 1971; Jan, May, and Sept 1972 excluded) (Gallagher, 1977). The substratum at all stations was sand or sand-shell, lacking attached vegetation. Station I was located in an area of high wave energy on the beach terrace; sediments were fine to very fine, moderately well-sorted, gray terrigenous sands (type 1), often very compacted. Station II was offshore of Station I in a "trough" between the beach terrace and Pierce Shoal; sediments were very coarse, poorly sorted sands containing very little mud (type 2), sometimes with numerous large shell fragments; mean particle size in sediment samples at Station II fluctuated between those of Stations IV and V, indicating patchiness in that area. Station III, located atop Pierce Shoal, was farthest offshore (2 mi) but was the shallowest station; sediments were medium-grained, moderately well-sorted calcareous sands (type 3); large shell fragments, common in the trough, were absent at Station III. Station IV was located in the trough

Table 1. Coordinates and mean depths of benthic stations.

Station	Coordinates*	Mean depth (m)
I	27°21.3'N, 80°14.1'W	8.4
II	27°21.6'N, 80°13.2'W	11.2
III	27°22.0'N, 80°12.4'W	7.1
IV	27°20.7'N, 80°12.8'W	10.9
V	27°22.9'N, 80°13.9'W	10.8

*U.S.C.G.S. Chart No. 1247, dated 1969.

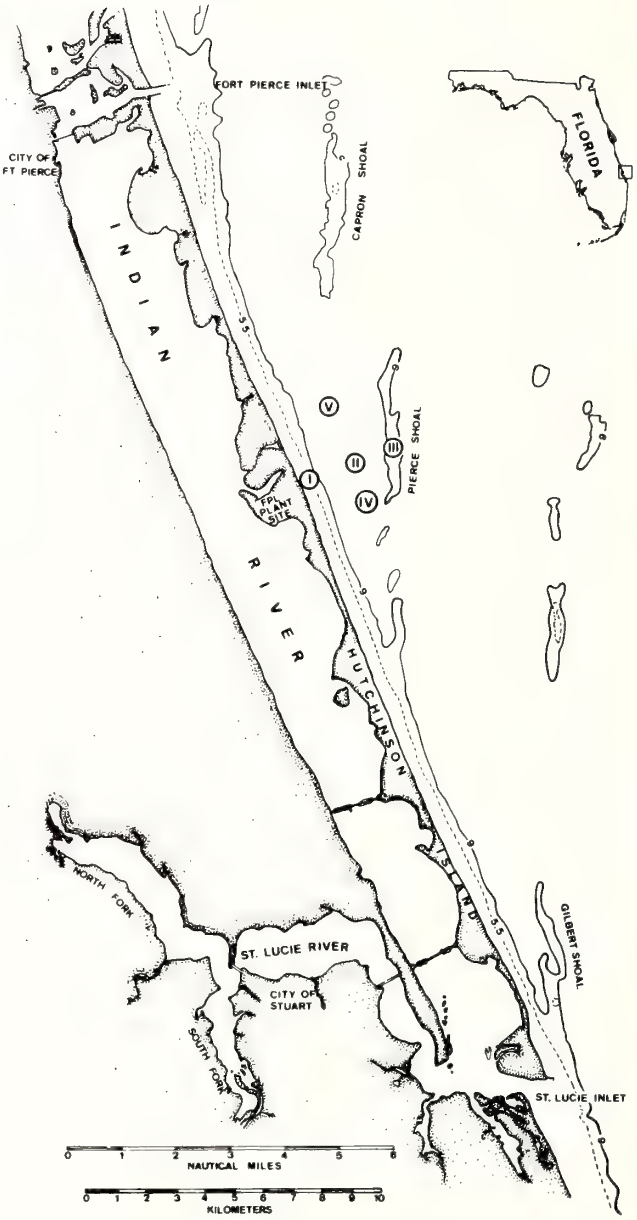


Fig. 1. Location of offshore benthic sampling stations at Hutchinson Island, central Florida east coast; depth contours in meters.

south of Station II; sediments were very similar to those at Station II (type 2), but sands were slightly less coarse; large shell fragments also were present. Station V, another trough station, was located north of Station II; sediments were very coarse, poorly sorted, slightly muddy, calcareous sandy-shell gravels (type 4).

Samples were preserved in 10% buffered formalin when collected and then were washed through a 0.71 mm U.S. Standard Sieve screen. Materials retained on the screen were preserved in alcohol, sorted to higher taxonomic categories using a binocular dissecting microscope, and transferred to specialists for identification and enumeration. I examined all mollusks from the samples and prepared a technical report on species composition and abundance (Lyons, in press). The specimens are deposited in the FDNR Marine Invertebrate Collection at St. Petersburg, Florida.

Species were designated as characteristic of the study site based upon occurrence during at least 6 of the 12 sampling periods. Interstation similarities of the fauna were determined using Czekanowski similarity coefficients (Clifford and Stephenson, 1975) derived from raw bimonthly abundances (Q mode) of the characteristic species at each station (five replicate grabs pooled) during each of eight sampling periods when sediments were analyzed. Station sediments likewise were examined for similarity using percentages by weight of particle sizes (∅) of the samples during each of the same eight periods. Resultant dendrograms of similarity based on fauna and on sediments were compared for evidence of faunal affinity for sediment types.

RESULTS

One hundred thirty-six molluscan species comprising 4135 living specimens were collected with the benthic grab. Station I, which yielded only 40 specimens in 16 species during 11 sampling periods (one atypical sample excluded), was eliminated from further analyses. Station III, the shoal station, yielded 697 specimens in 23 species. Greatest abundance and diversity occurred at the trough stations: Station II—1139 specimens, 72 species; Station IV—841 specimens, 79 species; Station V—1418 specimens, 70 species. By class, 54 bivalve species contributed 75.5% of all specimens, followed by 78 gastropods (18.4%), 3 polyplacophorans (5.2%), and 1 scaphopod (0.9%). Identities and abundances of all species were reported elsewhere (Lyons, in press).

Only 33 of the 136 species (24%) were collected during at least 6 of the 12 sampling periods, but those characteristic species contributed 90% of all specimens obtained during the study. The characteristic species, which included 16 bivalves, 13 gastropods, 3 polyplacophorans, and 1 scaphopod, contributed greater proportions of the total fauna at Stations III and V than at Stations II and IV (Table 2).

Czekanowski similarity coefficients derived from abundances of the characteristic species were used to construct a dendrogram of relationships among samples collected at Stations II-V during eight sampling periods (Fig. 2). Three groups were evident: one group contained all of the Station III samples, one contained six Station II samples and seven

Table 2. Abundance and frequency of occurrence of characteristic molluscan species in grab samples, Hutchinson Island Stations II-V, Sept 1971 - July 1973 (n = number of specimens; m = number of months of occurrence).

					Station					
Species	Total		II		III		IV		V	
	n	m	n	m	n	m	n	m	n	m
Crassinella lunulata (Conrad, 1834)	1373	12	367	10			117	7	889	12
C. dupliniana (Dall, 1903)	580	12	55	10	458	12	51	10	16	6
Chione intapurpurea (Conrad, 1849)	350	12	137	12	12	7	107	10	94	9
Caecum cooperi S. Smith, 1860	189	12	69	11	37	8	44	9	39	10
Glycymeris spectralis Nicol, 1952	148	12	13	6	82	12	52	10	1	1
Ischnochiton niveus Ferreira, 1987	123	12	47	10			47	9	29	10
Chione grus (Holmes, 1858)	110	6	5	2			67	2	38	5
Calyptraea centralis (Conrad, 1841)	84	12	29	7			37	11	18	8
Caecum strigosum de Folin, 1868	82	11	44	5			18	7	20	8
Chaetopleura apiculata (Say, 1834)	72	12	17	7			31	5	24	9
Arene tricarinata (Stearns, 1872)	66	10	17	7	1	1	18	6	30	5
Macoma brevifrons (Say, 1834)	55	12	21	9			21	8	13	8
Ervilia concentrica (Holmes, 1860)	49	6	4	1	43	5			2	2
Pleuromeris tridentata (Say, 1826)	44	10	16	4	10	7	13	6	5	2
Corbula barrattiana C.B. Adams, 1852	41	11	6	3			16	7	19	9
Graptacme calamus (Dall, 1889)	39	9	3	3	22	9	14	3		
Pteromeris perplana (Conrad, 1841)	37	12	10	6	1	1	25	11	1	1
Nucula proxima Say, 1822	31	10	7	3			2	2	22	8
Caecum floridanum Stimpson, 1851	25	10	12	8			13	6		
Abra aequalis (Say, 1822)	24	6	7	3			4	2	13	5
Polygyreulima sp. A	22	10	12	8			7	4	3	2
Finella adamsi (Dall, 1889)	21	6	11	3	2	2	4	2	4	2
Ischnochiton hartmeyeri Thiele, 1910	20	7	8	3			9	5	3	2
Suturoglypta iontha (Ravenel, 1861)	19	7	5	4			3	2	11	5
Astyris lunata (Say, 1826)	16	8	3	2			4	1	9	6
Nassarius consensus (Ravenel, 1861)	14	7	6	3			2	2	6	5
Chama congregata (Conrad, 1833)	13	9	3	2			7	5	3	3
Semele bellastriata (Conrad, 1837)	12	8	7	5			2	2	3	2
Semelina nuculoides (Conrad, 1841)	10	6	2	2	6	4	2	1		
Olivella floralia (Duclos, 1853)	9	7	1	1			3	2	5	5
Prunum roscidum (Redfield, 1860)	9	7					2	2	7	5
Tivela floridana Rehder, 1939	9	7	2	2	7	5				
Seila cf. *S. adamsi* (H.C. Lea, 1845)	8	7	2	2			1	1	5	5
Total specimens (33 spp.)	3704		948		681		743		1332	
Percent all specimens at station (128 spp.)	90.4		83.2		97.7		88.3		93.9	

Station IV samples, and one contained all Station V samples in addition to the two remaining Station II samples and one Station IV sample. Similarity coefficients derived from sediments produced a dendrogram with virtually the same groupings (Fig. 2). The two Station II samples that clustered with those of Station V were the same two samples placed there by species composition and abundance. Sediments of the atypical Station IV sample (IV-2) did not cluster with Station V sediments, but raw data values reveal that the sample contained approximately 5% more large shell particles than did other sediment samples at Station IV. That slight increase evidently was sufficient to support a species group more typically associated with sediments found at Station V.

The most abundant mollusks at Hutchinson Island were two species of the bivalve genus *Crassinella* (Crassatellidae). *C. lunulata* and *C. dupliniana* together constituted 47% of all specimens; considering only the characteristic species, that influence increased to 53%.

Crassinella lunulata was most abundant among the large shell particles in sediments of Station V but also was abundant occasionally at Stations II and IV. Of 367 *C. lunulata* recorded at Station II, 347 (95%) occurred in the two samples in which sediments were of the type found at Station V (see Fig. 2). At Station IV, 44 of 117 *C. lunulata* occurred in the sample with sediments that contained 5% more large shell particles, and 67 specimens occurred in one other sample. Sediments of the latter sample were not analyzed, but the associated fauna included large numbers of several other mollusks (e.g. *Chaetopleura apiculata, Chione grus*) typically associated with large shell particles. Thus, 95% of the *C. lunulata* at Station IV also occurred in two samples with sediments more similar to those at Station V. Together, the 12 Station V samples and the two samples each from Stations II and IV contained 98% of all *C. lunulata.* Seventy-nine percent of all *C. dupliniana* occurred among the well-sorted medium sands of Station III, and the remainder of the spec-

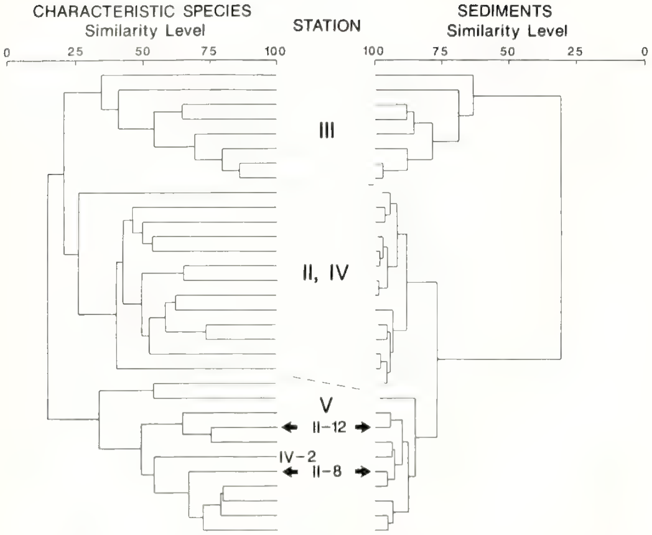


Fig. 2. Dendrograms of Czekanowski similarity coefficients (Q mode) based upon raw abundances of 33 characteristic species (left) and percent size composition of sediments (right), showing correspondence between species associations and sediments at four stations (II-V) sampled bimonthly, Sept 1971-July 1973 (4 months excluded).

imens were distributed among trough Stations II, IV, and V.

To test the dependence of the two *Crassinella* species on certain sediments, abundance data for each species were examined by station and by sediment type using samples collected during the eight periods when sediments were analyzed. As defined by Gallagher (1977), type 2 sediments occurred at Stations II (six samples) and IV (all samples), type 3 sediments occurred only at Station III, and type 4 sediments occurred at Station V (all samples) and occasionally at Station II (two samples). For this analysis, however, the November 1971 sample (IV-2) at Station IV was considered a type 4 sediment. Although sediments in that sample did not cluster with those at Station V, the sample did contain greater quantities of large shell particles, and the fauna clustered with fauna typical of Station V (Fig. 2). Species abundance data were equalized by converting to average catch per sample; each station was sampled eight times, so abundances at Stations III and V each were divided by 8, and combined abundances at Stations II and IV were divided by 16. Types 2, 3, and 4 sediments occurred in 13, 8, and 11 samples, respectively.

Relative abundances of the two species of *Crassinella* in eight samples at each station differed little from those in the total 12 samples (Table 3). However, average catch by sediment type demonstrated clearly the affinity of *C. lunulata* for type 4 sediments (Table 4).

Information on recruitment, growth, and longevity was discerned from size frequency distributions of the two *Crassinella* species. Height of the largest specimen of *C. lunulata* was 8.5 mm, but specimens seldom exceeded 6 mm except during September 1971 (Fig. 3). Small (<1.5 mm) juveniles occurred during all sampling periods except September 1971, suggesting some year-round recruitment into the population. Scarcity of small specimens in September 1971 samples is not understood. Such specimens must have been present in the study area to produce the 2-4 mm specimens common during following sampling periods. Bimodality of sizes during September 1972 and May and July 1973 indicates successful "sets" prior to those months, probably during spring through fall 1972 and spring 1973. Only a few individuals in September 1972 survived to sizes dominant in September 1971, and the 1971-72 year class never attained the maximum size of the September 1971 sample. However, the 1972-73 year class was very successful, and the larger size group of July 1973 probably would have attained maximum size by fall 1973. Together, the data indicate a life span of 12-18 months.

Height of the largest dead shell of *Crassinella dupliniana* was 3.4 mm, but no living specimens larger than 2.8 mm were obtained (Fig. 4). Smallest specimens (1.0-1.2 mm) occurred during May through November of each year, indicating recruitment during warm months, and largest specimens (2.6-2.8 mm) usually occurred in May and July. Although cohort growth progressions among intermediate sizes (1.3-2.5 mm) were less evident, *C. dupliniana* recruits seemed to grow to 2.5-2.8 mm in about 12 months, and maximum size (3.4 mm) probably was attained by specimens that survived for a few more months.

DISCUSSION

Although the 136 species of mollusks collected in sand-shell substrates off Hutchinson Island suggest a diverse fauna, most species were relatively rare. Some species were scarce

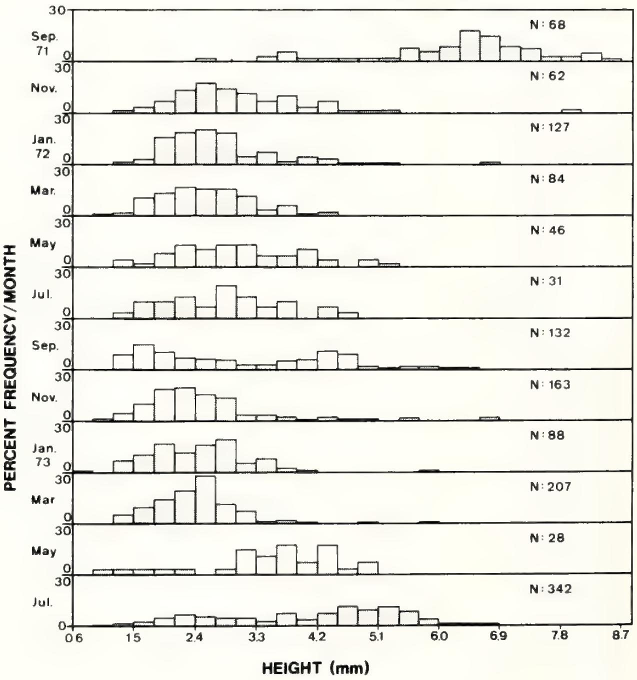


Fig. 3. Size frequency (0.3 mm increments shell height) of *Crassinella lunulata* at Hutchinson Island, Sept 1971-July 1973.

Table 3. Relative abundance (%) of *Crassinella dupliniana* and *C. lunulata* in 12 and 8 bimonthly samples at Hutchinson Island benthic stations (catch combined for stations II and IV).

	Total Specimens (100%)		% Occurrence by Station					
			II, IV		III		V	
Species	12 mo.	8 mo.	12 mo.	8 mo.	12 mo.	8 mo.	12 mo.	8 mo.
C. dupliniana	580	365	18.3	19.2	79.0	77.5	2.8	3.3
C. lunulata	1373	1006	35.3	40.7	0.0	0.0	64.7	59.3

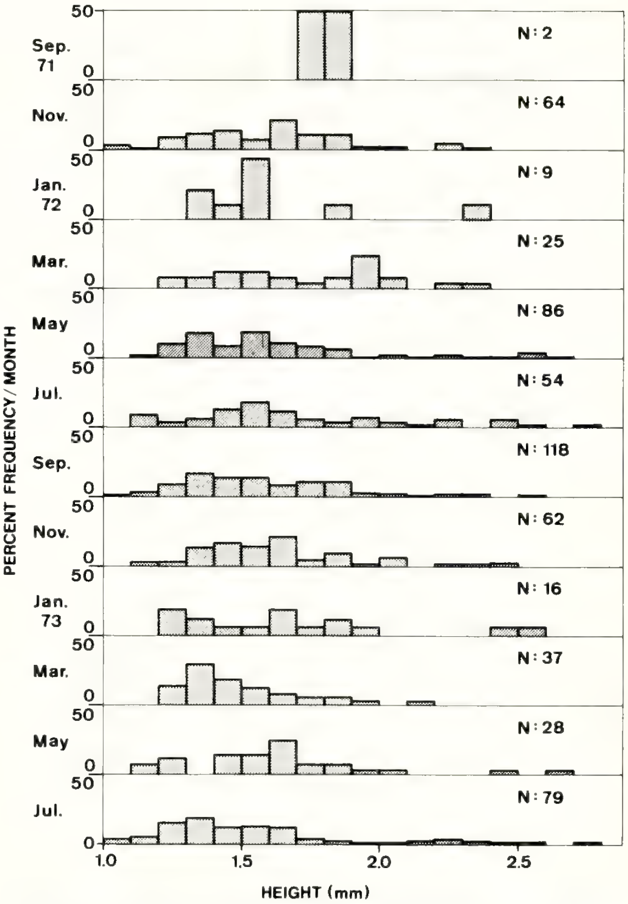


Fig. 4. Size frequency (0.1 mm increments shell height) of *Crassinella dupliniana* at Hutchinson Island, Sept 1971-July 1973.

representatives from nearby estuarine and deeper offshore assemblages, and others were juveniles of tropical forms that recruited to the area via the nearby Florida Current during spring and summer but died during fall and winter. However, most rare taxa seemed to be shallow shelf species typically affiliated with hard substrata. Many of those species associate with algae or sponges that exist, within the study area, principally on the scarce and widely scattered shells of larger dead mollusks (e.g. species of *Mercenaria, Busycon, Pleuroploca, Hexaplex,* and *Argopecten*). Expectedly, the scattered hard-substratum habitat was not sampled adequately with the grab.

Sediments at the study site are typical of those that border the coast of east central Florida. The shallow shelf is a submerged sedimentary plain, generally of low relief but with ridge-like linear shoals resting on the seaward-dipping platform (Meisburger and Duane, 1971). The linear shoals form a small angle (most $<35^{0}$) with the coast line and open northward (Fig. 1). Such shoals usually are formed at the shore-face in response to interactions between south-trending, wind-driven surface currents and wave-generated bottom currents during winter storms. Offshore shoals represent previous shore-face shoals detached by landward erosion (Duane *et al.*, 1972). Sediment types at the shoal and on the surrounding bottom in the study area essentially are the same as those that occur throughout the inshore region between St. Lucie Inlet and Cape Canaveral, Florida (Meisburger and Duane, 1971; Duane *et al.*, 1972).

The 33 characteristic species found in the coastal oceanic environment at Hutchinson Island constitute a typical molluscan assemblage of small forms adapted to sand and shell-hash bottom sediments. However, differences in sediment composition strongly influenced the distributions of species in that environment. The hard-packed fine to very fine sands of the beach terrace supported a very sparse fauna, but 8 of the 16 species collected there did not occur further offshore. The consistently well-sorted medium sands of the offshore shoal also supported relatively few species, but unlike the beach terrace, several species were abundant there. The bivalves *Crassinella dupliniana, Glycymeris spectralis, Ervilia concentrica, Semelina nuculoides,* and *Tivela floridana*, and the scaphopod *Graptacme calamus*, were much more abundant at the shoal than elsewhere. Except for *E. concentrica*, those species generally are scarce or absent in most Florida sand-bottom assemblages but probably occur at other offshore shoals along east central Florida. Characteristic species associated with large shell particles in the trough included the bivalves *C. lunulata, Nucula proxima,* and *Abra aequalis*, and several gastropods. Reasons for the occurrence of *C. lunulata* are discussed subsequently. *N. proxima* and *A. aequalis* are deposit feeders that ingest fine particles trapped among the very coarse sediments. Gastropods such as *Suturoglypta iontha, Astyris lunata, Prunum roscidum,* and *Seila* cf. *S. adamsi* utilize the coarse sediments for shelter and feed upon other organisms associated with those sediments. The more heterogeneous sediments in other trough samples supported more species than did sediments with large shell fragments. Species associated with those sediments included a bivalve, *Chione intapurpurea*, and several sand-dwelling gastropods, e.g. *Caecum cooperi, C. floridanum, C. strigosum,* and *Finella adamsi.*

The dependence of species on particular sediments

Table 4. Average ($\bar{x}$ N) and relative abundance (%) of *Crassinella dupliniana* and *C. lunulata* in 8 bimonthly samples, by station and sediment type.

	Station			Sediment Type		
Species	II, IV	III	V	2	3	4
			$\bar{x}$ Specimens/Sample			
C. dupliniana	4.4	35.4	1.5	3.5	35.4	3.3
C. lunulata	25.6	0.0	74.6	1.4	0.0	89.8
			% Occurrence			
C. dupliniana	19.2	77.5	3.3	12.6	77.5	9.9
C. lunulata	40.7	0.0	59.3	1.8	0.0	98.2

is exemplified by the two most abundant bivalves, *Crassinella dupliniana* and *C. lunulata*. *C. dupliniana* was most abundant among the well-sorted medium sands of the offshore shoal and occurred less commonly in the trough. Although never as dominant as at the shoal, medium sands always were components of sediments at the trough stations and evidently occurred there in quantities sufficient to support lesser numbers of *C. dupliniana*. Conversely, *C. lunulata* did not occur at all atop the shoal but was abundant in sediments with large shell particles in the trough. Only one juvenile specimen of *C. lunulata* and no *C. dupliniana* occurred on the compacted fine to very fine sands of the beach terrace. Harry (1966) documented the affinity of *C. lunulata* for sediments with a high percentage of coarse shell particles. *C. mactracea* (Linsley, 1845), a species very similar to *C. lunulata* in morphology and maximum size, lives in gravel communities from New York to Massachusetts (Allen, 1968). Both species use a delicate byssus to attach to surface substratum (Harry, 1966; Allen, 1968). Harry (1966) speculated that *C. lunulata* also may burrow. However, specimens of *C. lunulata* in most environments are of similar size or slightly larger than the shell fragments among which they live. Consequently, it seems reasonable to propose that *C. lunulata* lives almost interstitially among the large shell fragments, which might provide support, protection from predators, and camouflage. The smaller species, *C. dupliniana*, might derive similar benefits among sediments of correspondingly smaller size.

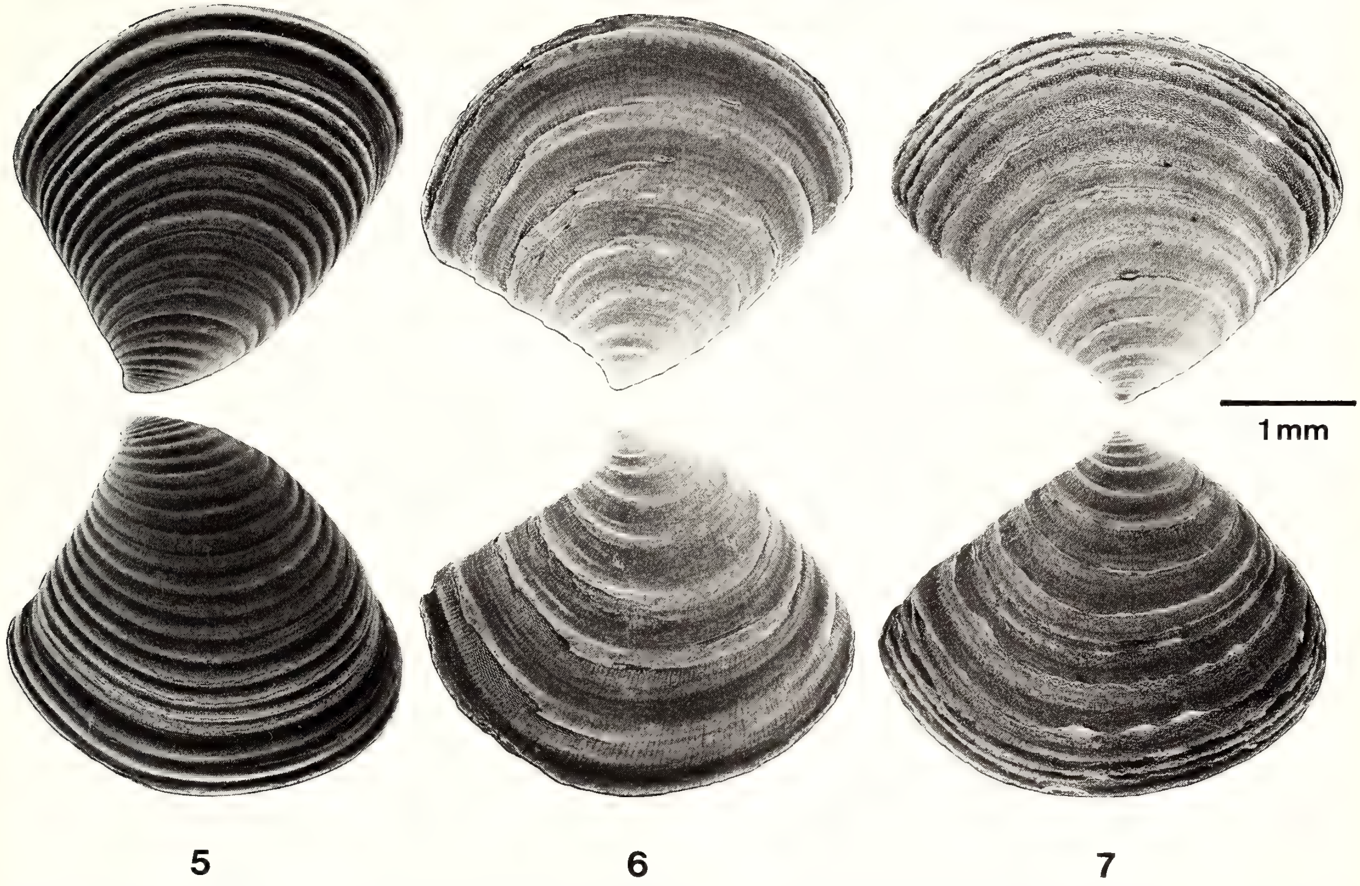
The requirement for settlement on certain sediments poses a recruitment problem for larvae of many bivalves. *Crassinella dupliniana*, especially, could have a problem because its preferred sediment, well-sorted medium sands, occurs principally on the relatively uncommon shoals that border the coast. Larvae generally distributed in the eddy circulation over the eastern Florida shelf might have little chance of encountering those shoals. Some mollusks with special habitat requirements solve the recruitment problem by abbreviating or eliminating the planktonic larval period. Harry (1966) proposed that some Crassatellidae, e.g. *C. lunulata* and *Eucrassatella speciosa* (A. Adams, 1852), brood eggs at least during early development. *Cuna dalli* Vanatta, 1904, a species sometimes placed in Crassatellidae (Moore, 1957) and sometimes in Condylocardiidae (Abbott, 1974), has been demonstrated to be ovoviviparous (Moore, 1961). Partial or complete ovoviviparity that shortens or eliminates the planktonic larval period of *Crassinella* species would assure that young were released at or near appropriate sediments. The fact that most small juvenile *Crassinella* at Hutchinson Island occurred in the same sediments occupied by adults supports that hypothesis.

Unfortunately, no evidence of broodings can be obtained from the specimens of *Crassinella* used in this study. The specimens were examined in 1975 and were not inspected for evidence of brooding then. The 1953 living specimens of the two species were accompanied by 12,762 paired valves of dead specimens. Because most dead specimens were sealed and appeared fresh, it was necessary to dry and open the specimens to discern the incidence of live-collected material; most tissues were damaged or destroyed during that process.

Recruitment of both *Crassinella* species occurred at Hutchinson Island during much of the year. Egg-bearing *C. lunulata* have been reported off eastern Florida during September and off Texas during October (Harry, 1966). A September spawn supports the fall recruitment of *C. lunulata* suggested by some size frequency data from Hutchinson Island, but earlier spawns during other warm months by *C. lunulata* and by *C. dupliniana* also are indicated.

Crassinella dupliniana increases to five the number of Recent species recognized in the northwestern Atlantic Ocean. Harry (1966) recognized only two Recent species of northwestern Atlantic *Crassinella, C. lunulata* and *C. martinicensis* (d'Orbigny, 1846); Abbott (1974) followed Harry's classification. However, Allen (1968) maintained that the southern *C. lunulata* and the northern *C. mactracea* are separate species, although he did not mention characters which distinguish them. Because the status of those two taxa is uncertain, I maintain them separately here. *C. lunulata* occurs either from Massachusetts (Abbott, 1974) or from North Carolina (Allen, 1968) to Florida, Texas, Bermuda, and Brazil. Most recently, Coan (1984) recognized *C. aduncata* Weisbord, 1964, originally described as a Pliocene fossil, among the living fauna of the Caribbean Sea.

Because *Crassinella dupliniana* has not been reported in literature on Recent mollusks, it is illustrated here and compared with congeners. In a paper submitted in 1975, Ward and Blackwelder (1987) stated that the type specimen of *C. dupliniana* might be lost, but I examined syntypes (USNM 114922) at the National Museum of Natural History which are identical to the Hutchinson Island specimens. Although dissimilar in outline to most other species of the genus, *C. dupliniana* shares with them the external cellular texture, unique to shells of *Crassinella*, described by Harry (1966) and



Figs. 5-7. Left (upper) and right (lower) valves of three species of *Crassinella* from Florida. **5.** *C. dupliniana*, height 2.8 mm, Hutchinson Island Station IV, July 1972. **6.** *C. lunulata*, height 2.7 mm, Hutchinson Island Station II, January 1972. **7.** *C. martinicensis*, height 2.7 mm, off Clearwater, Florida, depth 44 m. All specimens deposited in FDNR Marine Invertebrate Collection.

Coan (1979). *C. dupliniana* (Fig. 5) is much smaller and has a more acute apical angle than *C. lunulata* and *C. mactracea.* The height of Dall's largest specimen of *C. dupliniana* was 3.2 mm and that of the largest specimen from Hutchinson Island was 3.4 mm, whereas maximum heights of *C. lunulata* and *C. mactracea* approach 10 mm (Allen, 1968). Valves of *C. lunulata* (Fig. 6) are quite compressed and have about 3 broad concentric ridges per millimeter of shell height, whereas valves of *C. dupliniana* are more swollen, and concentric ridges are finer and more closely spaced, averaging 6-7 per millimeter. *C. martinicensis* (Fig. 7), a species that occurs off both Florida coasts in 20-80 m depths, resembles the broadly triangular *C. lunulata* and *C. mactracea* more than it does the acute *C. dupliniana.* Harry (1966) reported a maximum height of 2.7 mm for *C. martinicensis*, but Florida specimens attain a maximum height of about 3.0 mm. Valves of *C. martinicensis* have 4-5 concentric ridges per millimeter of height; the ridges often are spaced irregularly, and several secondary ridges sometimes occur between them.

Crassinella dupliniana most resembles certain specimens of *C. nuculiformis* Berry, 1940, a narrowly ovate, inflated species that occurs from Baja California to Ecuador (Coan, 1979). The 2.9 mm valve of *C. nuculiformis* illustrated by Coan (1979: fig. 10) is strikingly similar to those of *C. dupliniana.* Coan (1979) noted that *C. nuculiformis* attains a height of 6.4 mm, but specimens from the upper Gulf of California (including the specimen in his fig. 10) were smaller, generally <3 mm. According to Coan (1984), *C. nuculiformis* is very similar to *C. maldonadoensis* (Pilsbry, 1897) from Uruguay to Argentina in the southwestern Atlantic, but the latter species has less prominent umbones and its concentric ribs fade more quickly toward the ventral margin. *C. adamsi* Olsson, 1961, an eastern Pacific species that attains a height of 3.6 mm, also is ovate but is proportionally longer than *C. nuculiformis* and *C. dupliniana*. Olsson (1961) mentioned an undescribed species similar to *C. adamsi* from the Caribbean coast of Panama. That species probably is *C. aduncata*, which differs from *C. adamsi* ''in attaining a larger size, having a more abrupt posterior slope, and . . . more prominent concentric ribs'' (Coan, 1984: 165).

In addition to the Hutchinson Island material, I have examined specimens of *Crassinella dupliniana* from off Cape Canaveral, Florida, from the Gulf of Mexico off western Florida (both FDNR Marine Invertebrate Collection), and from beach drift at Hunting Island State Park, South Carolina. These records indicate that *C. dupliniana* probably lives among appropriate sediments throughout much of the warm-temperate Carolinian Province.

Information on sediment associations of the two *Crassinella* species could prove useful for interpreting paleoenvironments. *C. lunulata* (Conrad, 1834), originally described as a fossil from the Pliocene Yorktown Formation of Suffolk, Virginia, occurs extensively in Pliocene and Pleistocene deposits of the southeastern United States (Gardner, 1944). *C. dupliniana* (Dall, 1903), originally described from the Pliocene Duplin Formation (now considered Yorktown) of Natural Well, Duplin County, North Carolina, also has been reported from Pliocene and early Pleistocene deposits in Virginia, the Carolinas, and north and south Florida (Dall, 1903; Mansfield, 1931, 1932; Gardner, 1944; Dubar and Taylor, 1962; Stanley, 1986; Ward and Blackwelder, 1987). High incidence of either species in Neogene strata probably would indicate environments similar to those with which they associated at Hutchinson Island.

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TEMPORAL VARIATION IN MICROSTRUCTURE OF THE INNER SHELL SURFACE OF *CORBICULA FLUMINEA* (BIVALVIA: HETERODONTA)

ANTONIETO TAN TIU
HARBOR BRANCH OCEANOGRAPHIC INSTITUTION
DIVISION OF APPLIED BIOLOGY
5600 OLD DIXIE HIGHWAY
FT. PIERCE, FLORIDA 34946, U.S.A.
ROBERT S. PREZANT
DEPARTMENT OF BIOLOGY
INDIANA UNIVERSITY OF PENNSYLVANIA
INDIANA, PENNSYLVANIA 15705, U.S.A.

ABSTRACT

Temporal variation of shell microstructure with emphasis on the inner shell surface was examined in caged and noncaged *Corbicula fluminea* (Müller) from the Leaf River, Mississippi. Shell structure in the outer shell layer, overlain by the periostracum, exhibited distinct seasonal variation from crossed-lamellar in warmer months to structures resembling cone complex crossed-lamellar in cooler months. Other variations associated with season were subtle, involving only the inner shell surface microstructures, such as replacement of well developed lamellae in warmer months by pitted, deformed or reticulate microstructures in cooler months. The shell microstructure ventral to the pallial line is of possible use in taxonomic and phylogenetic analyses of the Corbiculacea and could also be of value as an environmental monitor because the microstructures in this region were less variable than those dorsal to the pallial line.

Previous workers [i.e. Carter (1980)] have hypothesized that major variations in shell microstructures among bivalves are largely biologically controlled (i.e. more or less independent of environmental influences) and have developed adaptive edges towards resistance to abrasion or fracture, energy economies of secretion, etc. There are however exceptions to this generalization. Lutz and Rhoads (1979, 1980) and Lutz and Clark (1984) demonstrated that the microstructure of the inner shell layer of *Geukensia demissa* (Dillwyn) varied with season and latitude. Moreover, Tan Tiu and Prezant (1987) have shown that variation in the microstructure of the inner shell surface of *G. d. granosissima* (Sowerby) occurred within a small geographical area. Likewise, ultrastructure of the inner shell surface in *Polymesoda caroliniana* (Bosc) can reflect seasonal and/or habitat variation (Tan Tiu, 1987, 1988). Thus, environmental variation can directly or indirectly influence the deposition of shell microstructural components resulting in at least surficial modifications.

A brief review of bivalve shell microstructural studies will reveal the phylogenetic and ecological importance of such structural variations. The information derived from environmental modification of bivalve shell microstructure can help in understanding not only molluscan phylogeny (Carter, 1980), but also the historical (perhaps paleontological) events that brought about these changes (Lutz and Rhoads, 1980; Rhoads and Lutz, 1980). Realization of the full potential of shell microstructure patterns as a taxonomic tool and as a recorder of environmental change, depends on examination of bivalve shell microstructural variations (Carter, 1980). This paper reports temporal variations in the microstructure of the inner shell surface of caged and noncaged *Corbicula fluminea* (Müller) in the Leaf River, Belleville, Perry County, Mississippi, U.S.A.

MATERIALS AND METHODS

Caged and noncaged specimens of *Corbicula fluminea* were sampled seasonally from the south bank of the Leaf

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River (Belleville, Perry County, Mississippi) from June 1985 to June 1986. Additional noncaged samples were collected in October 1985 and January 1986. Dates of collection and number and lengths of specimens examined are presented in Table 1.

The source of caged samples was a "natural" population of *Corbicula fluminea* collected in June 1985 from the same site in the Leaf River. Forty-five marked clams were placed in each of eight cylindrical wire cages made of galvanized iron (30 cm long, 20 cm diameter, 0.7 cm mesh) and returned to the original collecting site in the Leaf River. Each cage was fastened to an iron pole using wires, and cages were set about two meters apart. Each pole was forced into the substratum, the bottom of the attached cage touching or slightly below the surface of the substratum.

Clams from each of two cages were shucked in the field at seasonal intervals (Table 1) and the shells were fixed separately in absolute ethanol. Select fractured and unfractured shell samples were dried in a Denton DCP-1 critical point drier using liquid CO_2 as a transfer agent, mounted on aluminum stubs using silver paint, coated with gold in a Polaron SEM Coating Unit E5100, and examined at 30 KV using an AMR 1000A scanning electron microscope. Nine areas of the inner shell surface were examined and compared, from the ventral shell margin to the umbo (Fig. 1). Whenever possible, terminology of microstructures of inner shell surfaces correlated with that proposed by Carter and Clark (1985).

Several biological and environmental variables were measured (Tan Tiu, 1987) but only monthly temperature of bottom water (± 1°C) in the Leaf River is presented here.

RESULTS

A. SHELL MICROSTRUCTURE

Microstructure of the inner shell surface varied distinctly from the ventrum (Area A) to the dorsum (Area I) (Figs. 2 - 10), but not along the curved anterior posterior axis. Distinct as well as subtle seasonal variations in the microstructure of the inner surfaces of shells are summarized in Table 2. With a minor exception presented below, there were no differences in the overall appearance and frequency of occurrence of microstructures of the inner shell surface in caged and noncaged *Corbicula fluminea* (Table 2).

Table 1. Lengths (mm) of *Corbicula fluminea* from Leaf River, whose shell microstructures were examined by scanning electron microscopy.

Date	Mean ± 1 Standard Deviation	Range	Total Clams Examined
Caged			
Sept 85	25.3 ± 3.1	15.8 - 28.5	30
Dec 85	27.7 ± 3.2	22.7 - 35.8	29
March 86	30.4 ± 2.8	26.1 - 37.9	30
June 86	30.3 ± 0.9	29.0 - 31.6	10
Noncaged			
June 85	21.9 ± 2.2	18.0 - 24.8	10
Sept 85	19.1 ± 4.5	10.3 - 23.7	10
Oct 85	24.2 ± 10.0	9.5 - 38.0	28
Dec 85	23.8 ± 7.6	12.5 - 37.6	10
Jan 86	25.0 ± 7.3	10.1 - 38.0	10
March 86	29.4 ± 4.5	21.5 - 38.0	9
June 86	31.9 ± 1.9	27.8 - 34.0	10

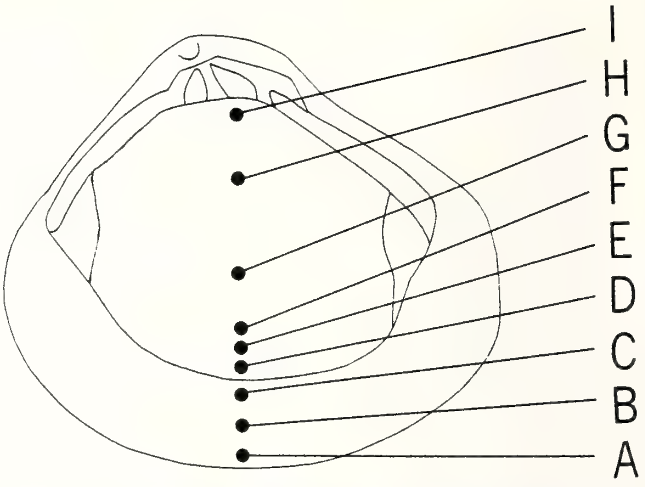
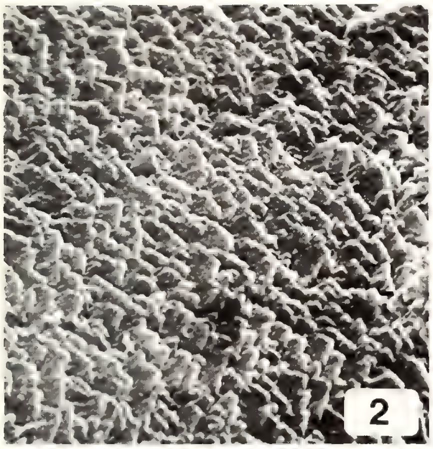


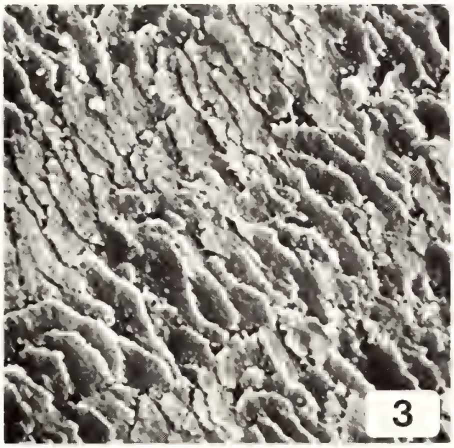
Fig. 1. Right valve of *Corbicula fluminea*. Areas of the shell surface examined are marked by dots, corresponding to the letters on the right: A, internal surface area overlain by periostracum; B, area just dorsal to Area A; C, area between Area B and pallial line; D, E, and F, the "transition zone"; G, area at the level of ventral margin of adductor scars; H, area at the level of dorsal margin of adductor scars; I, area near umbo.

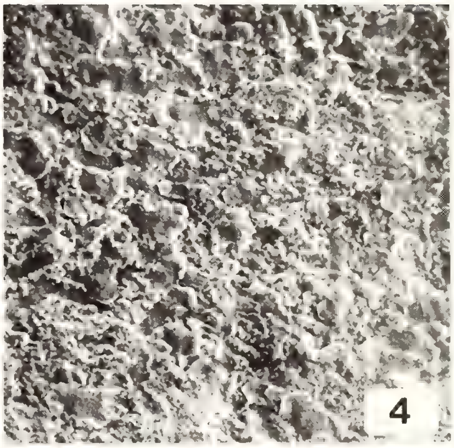
1. OUTER SHELL LAYER

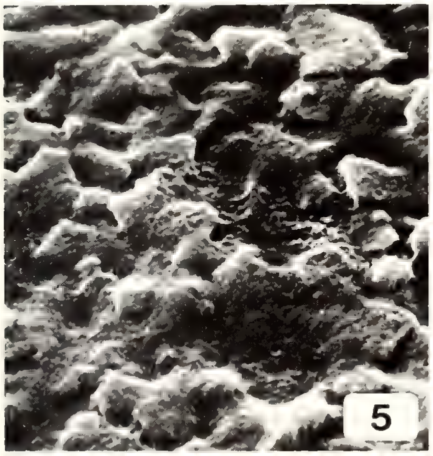
a. Area Overlain by Periostracum (Area A). Microstructure of the inner shell surface in the area overlain by the periostracum can be divided into Crossed-Lamella One and Microstructure C. Tertiary lamellae are apparently not organized into broad secondary lamellae in Crossed-Lamella One (Fig. 2). The first order lamellae in Crossed-Lamella One are less than 40 μm wide, and are arranged diffusely. The shell structure of Crossed-Lamella One approaches the medium diffuse crossed lamellar structure of Carter and Clark (1985). Microstructure C is a term of convenience that refers collectively to spiral, pseudospiral or rosette arrangements of laths surficially composing the crossed lamellar shell structure in area A (Fig. 11). The secondary lamellae on the depositional shell surface are arranged continuously into a spiral in spiral crossed-lamellar structure, discontinuously or into opposing hemispheres (arcs) in pseudospiral crossed-lamellar structure, and into irregularly arranged curved lamellae in rosette crossed-lamellar structure. Spiral and pseudospiral crossed-lamellar structures have been previously described by Prezant and Tan Tiu (1986), and both structures approach the cone complex crossed lamellar structure of Carter and Clark (1985). While Crossed-Lamella One occurs throughout the year, Microstructure C is present only in cooler months (Oct to March 1986) (Table 2).

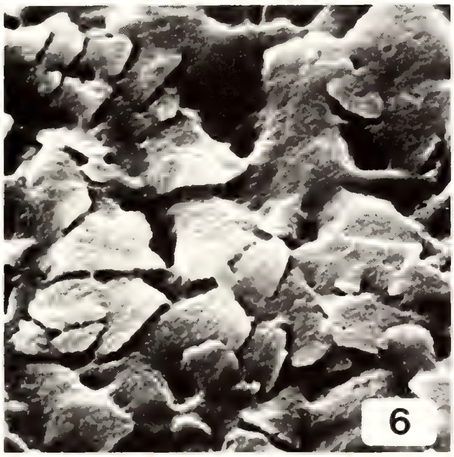
b. Areas Between Area A and Pallial Line (Areas B and C). Laths in area B are arranged more or less regularly into

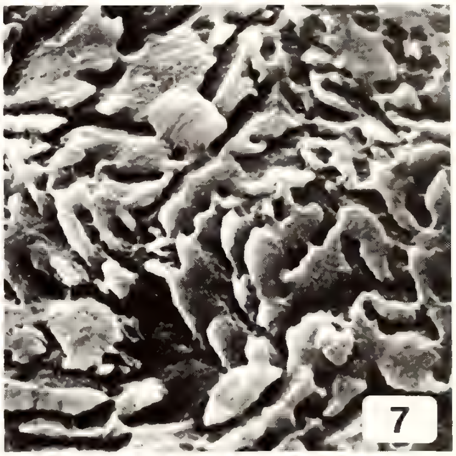


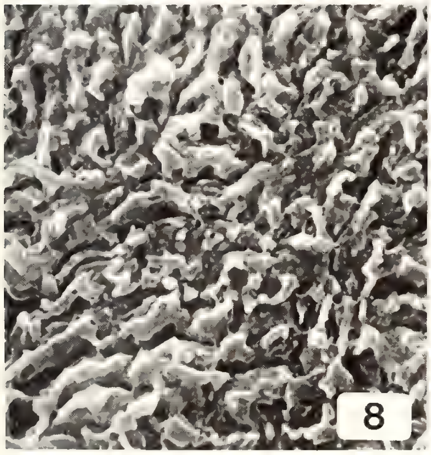


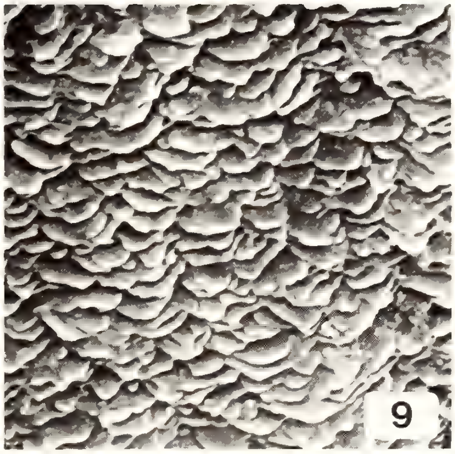












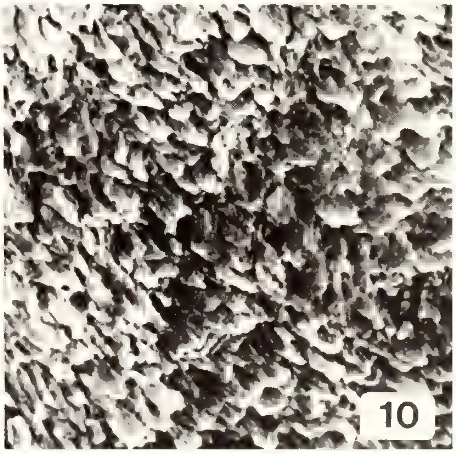


Fig. 2. Area A, overlain by periostracum, consisting of laths not organized into second order lamellae. Referred to as Crossed-Lamella One in the text [horizontal field width (HFW) = 14 μm]. **Fig. 3.** Area B, just dorsal to Area A consisting of secondary lamellae of opposing directions, together with Fig. 4 (Area C) make up Crossed-Lamella Two referred to in the text (HFW = 14 μm). **Fig. 4.** Area C, between Areas B and pallial line with overlying organic matrix (HFW = 14 μm). **Fig. 5.** Area D, just dorsal to pallial line (part of transition zone) consisting of narrow lamellae (HFW = 14 μm). **Fig. 6.** Area E, middle third of transition zone consisting of wide irregular lamellae (HFW = 14 μm). **Fig. 7.** Area F, just dorsal to Area E consisting of laths superimposed on irregularly fused lamellae (HFW = 14 μm). **Fig. 8.** Area G, at level of ventral margin of adductor scar consisting of irregularly fused lamellae that are perpendicular to shell surface. Referred to in the text as Complex Crossed-Lamella One (HFW = 14 μm). **Fig. 9.** Area H, at level of dorsal margin of adductor scar consists of overlapping broad lamellae, together with Fig. 10 (Area I) below is referred to as Complex Crossed-Lamella Two (HFW = 14 μm). **Fig. 10.** Area I, near umbo (where tubules are located) can be eroded (HFW = 14 μm).

second order lamellae, the latter in turn is arranged regularly to form first order lamellae less than 10 μm wide. Direction of the second order lamellae is opposite that of adjacent first order lamellae (Fig. 3). The shell structure in area B approaches the compressed crossed lamellar structure of Carter and Clark (1985). The laths in area C are irregularly arranged and apparently not organized into wide secondary lamellae as in Crossed-Lamella One. The boundaries of the first order lamellae are indistinct. Area C is often covered by an organic sheet that renders the underlying structures indistinct, except for the lamellar tips (Fig. 4). Microstructures of the inner shell surfaces in both areas A and B are referred to as Crossed-Lamella Two (Table 2). Loose or dense networks, which can be granulated, are distributed evenly or patchily in areas B and C. These networks are part of a continuum that is here referred to as Reticulate Microstructures (Fig. 12, Table 2). Frequency of occurrence of Reticulate Microstructures in areas B and C is variable (Table 2).

2. INNER SHELL LAYER

a. Areas of the Transition Zone (Areas D, E and F). These areas make up the transition zone, where the newly deposited laths, destined to become the inner complex crossed-lamella, are first formed over the pallial line. Incipient as well as narrow and thin laths are observed in area D adjacent to the pallial myostracum (Fig. 5). Laths that are broad and thick are often fused into irregular lamellae in Area E (Fig. 6). In area F, the lamellae are broader, with incipient laths over them (Fig. 7). The boundaries of first order lamellae on the depositional surface of the transition zone are indistinct. The structures composing the transition zone can also be overlain with loosely arranged Reticulate Microstructures (Fig. 12). The latter is often very dense and obscures the underlying original structures. Lamellae of the transition zone are generally perforated, deformed (appearance similar to Fig. 13) or absent in December and March. Reticulate Microstructures in areas D - F did not show distinct seasonal variation. However, as in areas B and C, the frequency of occurrence of this microstructure increased when the frequency of occurrence of "well formed" structures (Figs. 5 - 7) in these areas decreased.

b. Areas Dorsal to the Transition Zone (Areas G, H and I). The shell structure in Area G, H and I is inconsistent, approaching either the irregular or cone complex crossed lamellar structures of Carter and Clark (1985). Appearance of the exposed lamellae of the inner surface of shell dorsal to the pallial line is also variable. Among the commonly observed microstructures, three are described here and conveniently named as Complex Crossed-Lamella One, Complex Crossed-Lamella Two, and again Reticulate Microstructure.

Many of the lamellae are nearly perpendicular to the inner surface of shell and are irregularly arranged in Complex-Crossed Lamella One (Fig. 8). This microstructure is present in June and absent in December in both caged and noncaged clams.

The exposed ends of the lamellae in Complex Crossed-Lamella Two are wide and broad, arranged such that they overlap, one on top of the other like shingles (Fig. 9); they also can be slightly eroded (Fig. 10). Seasonal frequency of occurrence of this microstructure was lower in caged than noncaged clams. When present in December and March, this microstructure was eroded and deformed.

The appearance of Reticulate Microstructure in Areas G to I varied. A loosely to densely packed thin stranded network with or without granulations was present in varying amounts throughout the year. In December and March samples, this network had thicker strands with few granulations (Fig. 12).

Tubules that penetrated the calcareous shell component were consistently observed in the early dissoconch shell. The shell tubules are filled with mantle extensions. The latter are at least occasionally bifurcate toward the shell exterior

Table 2. Temporal variation in microstructure of inner shell surface of *Corbicula fluminea* from Leaf River, Mississippi. Frequency of occurrence expressed in classes where 0 = 0, 1 = 1 to 20, 2 = 21 to 40, 3 = 41 to 60, 4 = 61 to 80 and 5 = 81 to 100%. C = Microstructure C, a collective new term for spirals, pseudospirals and rosettes; CL = Crossed-Lamella; RET = Reticulate Microstructure; TRP = Transition Zone Lamellae are present; TRA = Transition Zone Lamellae are absent; CCL = Complex Crossed-Lamella.

	Area A		Areas B-C		Areas D-F			Areas G-I		
	C	CL1	CL2	RET	TRP	TRA	RET	CCL1	CCL2	RET
Noncaged										
June 85	0	5	5	0	5	0	0	2	2	2
Sept 85	0	5	5	0	5	0	0	0	4	1
Oct 85	1	5	5	0	5	0	2	0	3	2
Dec 85	3	2	5	1	3	3	0	0	3	3
Jan 86	3	2	5	0	3	1	2	0	0	4
March 86	2	3	5	1	4	0	2	1	0	4
June 86	0	5	5	1	5	0	2	1	1	3
Caged										
Sept 85	0	5	5	0	5	0	1	2	1	2
Dec 85	3	3	5	1	3	1	1	0	2	3
March 86	3	3	4	2	3	0	3	0	1	5
June 86	0	5	4	2	4	0	4	2	0	4

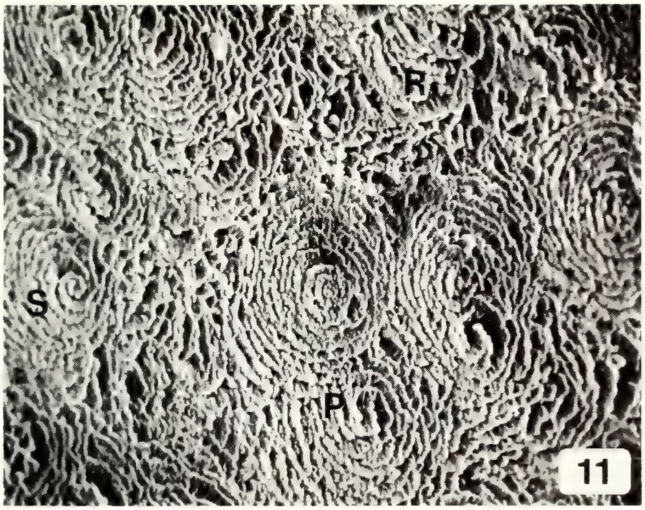


Fig. 11. Spiral (S), pseudospiral (P) and rosette (R) microstructures are present in Area A in both caged and noncaged clams during cooler months (HFW = 23 μm).

(Tan Tiu, 1987). Details of the microstructure and function of the tubules are reported in a separate paper (Tan Tiu and Prezant, 1988).

Some microstructures of the inner shell surface had low frequency of occurrences. An example of a microstructural variant whose frequency of occurrence was low (less than 20% of total samples) and did not show distinct seasonal variation is shown in figure 14. Lamellae in figure 14 are arranged in such a way that they resemble a pinwheel. Other examples of such variants are described by Tan Tiu (1987).

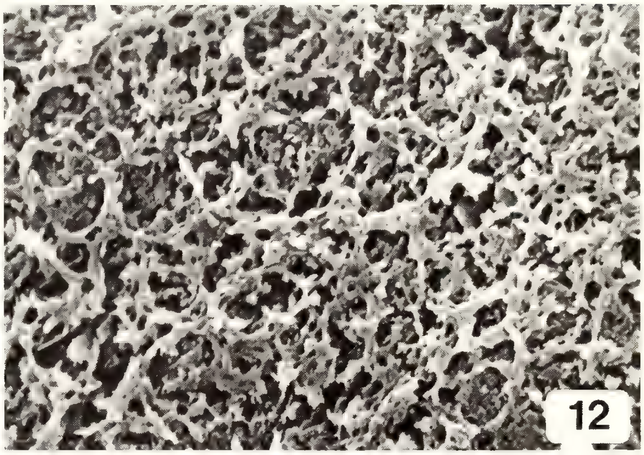
B. WATER TEMPERATURE

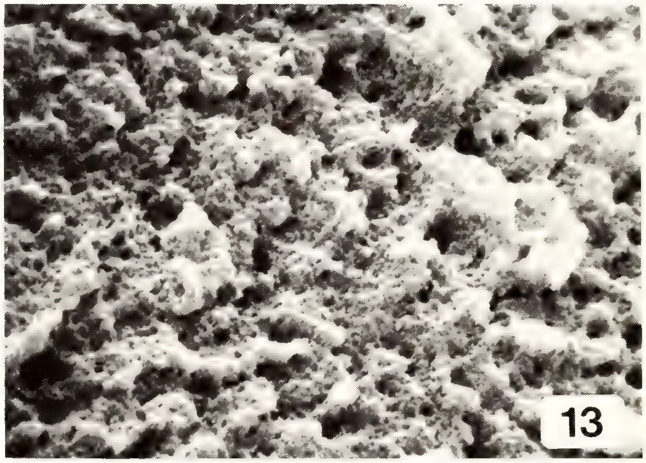
The temperature of the bottom water in the Leaf River was highest in August and lowest in January (Fig. 15). This was the only environmental variable that showed a distinct cyclic pattern.

DISCUSSION

The frequency of occurrence of Microstructure C in the outer shell layer and "well formed" lamellae in the transition zone of the inner shell layer of both caged and noncaged *Corbicula fluminea* exhibited seasonal variation. The time of occurrence of these microstructures; however, were different. Frequency of occurrence of Microstructure C was inversely associated with bottom water temperature, while the presence of "well formed" lamellae in the transition zone was positively associated with bottom water temperature.

Reticulate Microstructure observed in *Corbicula fluminea* is similar in appearance to that observed in *Polymesoda caroliniana* by Tan Tiu (1987, 1988). In both species, an increase in occurrence of Reticulate Microstructure corresponded with a decrease in occurrence of other microstructural "types" in the areas involved. Several studies have suggested that valve closure results in calcium reabsorption from the inner shell surface (Crenshaw and Neff, 1969; Lutz and Rhoads, 1979; Akberali and Trueman, 1985). During valve closure under stressful or normal conditions, bivalves shift to an anaerobic metabolic pathway to generate ATP (Hochachka, 1980). The resulting acidic by-products,





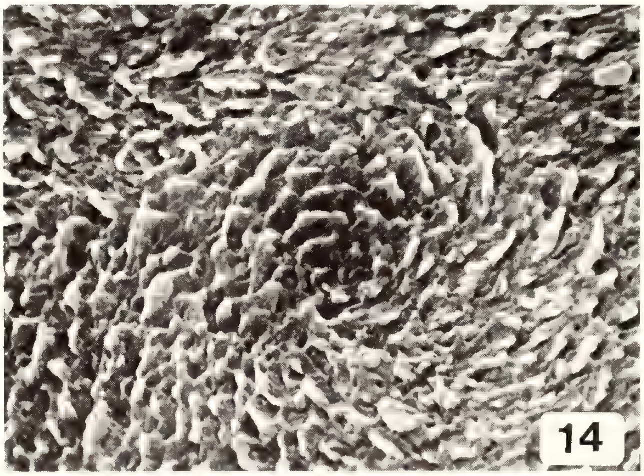


Fig. 12. Ultrastructure referred to as Reticulate Microstructure in the text (HFW = 21 μm). **Fig. 13.** Highly eroded lamellae predominating in cooler months in Areas G to I (HFW = 19 μm). **Fig. 14.** Pinwheel arrangement of laths (HFW = 21 μm).

such as succinate, propionate, etc., of this metabolic pathway are then buffered by carbonates in the calcareous shell resulting in shell dissolution (Akberali and Trueman, 1985). The Reticulate Microstructure with numerous spaces between structures, could be a result of dissolution of the inner surface of the shell consequent to valve closure as observed by Prezant *et al.* (1988) and as suggested by Akberali and Trueman (1985).

While seasonal variation in appearance of microstructures dorsal to the pallial line consists mainly of "well formed" lamellae in warmer months being replaced by deformed lamellae in cooler months, those microstructures ventral to the pallial line in area A are "well formed" throughout all seasons with Microstructure C predominating in cooler months. This suggests that Crossed-Lamella One and Microstructure C are inducible microstructures dependent on varying environmental conditions associated with change in season. Temperature of bottom water in Leaf River, which has a distinct seasonal cycle, could play a major role in this microstructural induction. The presence of "well formed" microstructures in all seasons ventral to the pallial line, but only in warmer months dorsal to the pallial line, suggests that shell growth is continuous along the shell margin, and periodic on the inner shell layer dorsal to the pallial line. This was expected since winter in Mississippi is relatively short, and water temperature in the Leaf River dropped below 10°C for only a short time. According to Fritz and Lutz (1986), shell growth of *Corbicula fluminea* in New Jersey occurs at water temperatures above 10°C.

Prezant and Tan Tiu (1986) discovered spiral crossed-lamellar microstructure in summer and winter samples of *Corbicula fluminea* from Strong River, Mississippi and pseudospiral microstructure in a winter sample of *C. fluminea* from Leaf River, Mississippi. These authors suggested a seasonality of occurrence of pseudospiral microstructures in Leaf River. Data presented here clearly indicate, for the first time, that spiral crossed-lamellar microstructures (Fig. 11) are found in *C. fluminea* in the Leaf River. Furthermore, spiral and pseudospiral crossed-lamellar microstructures were deposited only in cooler months by *C. fluminea* in the Leaf River. Similarity of occurrence of these microstructures in caged and non-caged Leaf River samples nullify the idea of Prezant and Tan Tiu (1986) that Leaf River samples possessing pseudospiral microstructure "drifted" per se from upstream habitats. Spiral crossed-lamellar microstructure does not occur in the closely related *Polymesoda caroliniana* or other corbiculids from other habitats (Prezant and Tan Tiu, 1986; Tan Tiu, 1987, 1988). Samples of *P. caroliniana* collected in cooler months, however, do exhibit a pseudospiral microstructure (Tan Tiu, 1987, 1988). *Polymesoda caroliniana* is the only other corbiculid with data on seasonal variation of shell microstructure (Tan Tiu, 1988). Data on *C. fluminea* and *P. caroliniana* suggest that although the microstructure at the internal shell margin overlain by periostracum exhibits seasonal variation, it has taxonomic and phylogenetic implications that warrant further consideration.

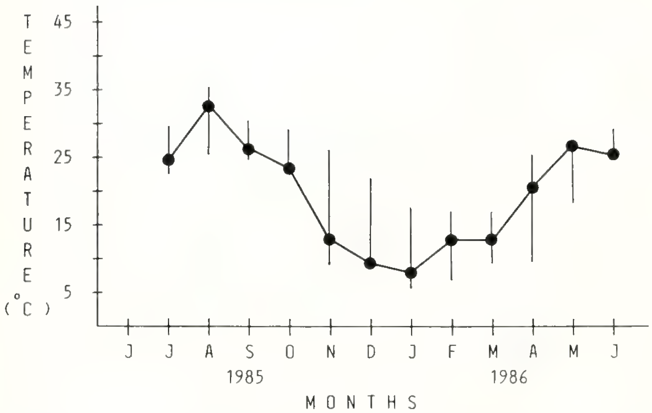


Fig. 15. Monthly variation in temperature of the bottom water of Leaf River at the collection site. Dots represent monthly records of water temperature at sampling time, while vertical lines through the dots represent monthly temperature ranges as measured by a maximum-minimum thermometer.

Dorsal to the pallial line, "well formed" structures predominating in warmer months are usually replaced by deformed or pitted structures in cooler months. This is similar to phenomena observed in other bivalves. Wada (1960) demonstrated that the size and shape of nacreous tablets composing the inner shell layer of the bivalve *Pinctada martensii* (Dunker) varied with season, being large and hexagonal in summer, and small, deformed and pitted during winter. Lutz and Clark (1984) showed that nacreous tablets of the inner shell layer of the Atlantic ribbed mussel *Geukensia demissa* varied not only with season but also with latitude. Further, Tan Tiu and Prezant (1987) showed that distinct differences in the shape and size of nacreous tablets along the inner surface of the inner shell layer of *G. d. granosissima* can occur even within a small geographical area. In *Polymesoda caroliniana,* Tan Tiu (1987, 1988) observed seasonal and spatial variations of microstructures in the inner surfaces of their shells. Because of high variability of the microstructure dorsal to the pallial line brought about by various factors, shell microstructure in this area has less taxonomic value than shell microstructure distal to the pallial line. The significance of the pinwheel arrangement of lamellae and other microstructural variations dorsal to the pallial line (Tan Tiu, 1987) is currently unknown.

The guide to shell structure proposed by Carter and Clark (1985) is clearly helpful in classifying shell structures and inferring phylogeny. However, in *Polymesoda caroliniana* (Tan Tiu, 1988) and *Corbicula fluminea*, where intrinsic or extrinsic intraspecific variability in shell structure occurs, the use of specific guides correlating specific taxa with specific shell microstructures could be misleading.

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THE FUNCTIONAL MORPHOLOGY OF THE ORGANS OF THE MANTLE CAVITY OF *BATISSA VIOLACEA* (LAMARCK, 1797) (BIVALVIA: CORBICULACEA)

BRIAN MORTON
DEPARTMENT OF ZOOLOGY
THE UNIVERSITY OF HONG KONG
HONG KONG

ABSTRACT

Batissa violacea (Lamarck) occurs in rivers of the tropical Indo-West Pacific. It superficially resembles members of the Unionidae but morphologically is clearly corbiculid. Like *Polymesoda, Batissa* exhibits pedal gape feeding and can dig to considerable depths, probably to avoid desiccation. *B. violacea* is dioecious, grows to 150 mm in shell length and is probably long-lived. The Corbiculidae are considered recent immigrants to fresh waters. A relatively unspecialized morphology and reproductive strategy but with physiological and behavioural specializations to avoid drought have allowed this. Reproductive specialisation characterises *Corbicula*, occupying river head-waters and lentic systems. *Batissa* and *Polymesoda* thus provide living examples of how fresh waters have been colonised by the Corbiculidae.

The Corbiculacea is a group of fresh or brackish water heterodonts, mostly tropical in their distributions. Most interest is with *Corbicula*, particularly the exclusively freshwater *C. fluminea* (Müller) that has been spread artificially from its Asian range to North and South America and Europe (Morton, 1986). In North America it is a pest of power station cooling systems which it clogs, although other problems have been encountered such as the blockage of drainage canals (McMahon, 1983). Species of *Polymesoda* in both the western Pacific and western Atlantic are similarly tropical and occur in salt marshes and mangroves of estuaries (Morton, 1984). They too have elicited interest for their physiological adaptations to the harsh high intertidal (Depledge, 1985).

Prerequisite to an understanding of the species of Corbiculacea is anatomy, especially since the representatives of this group appear to be phenotypically highly variable, e.g. *C. fluminea* (Britton and Morton, 1986; Morton, 1987a). Few authors have reported details of corbiculid anatomy. Prashad (1920) described briefly the gross anatomy of *Corbicula fluminalis* (Müller) and Dinamani (1957) that of *Villorita cyprinoides* (Gray). Details of the anatomy of *C. fluminea* are reported upon by Kraemer (1978, 1979, 1981), Kraemer and Lott (1978) and Britton and Morton (1982). Morton (1976) has described the anatomy of *Polymesoda (Geloina) erosa* (Solander). There have been few studies of the genus *Batissa*, most information resulting from geographic collections. Raj and Fergusson (1980), however, have investigated the osmolarity and ionic composition of the blood of *Batissa violacea* (Lamarck, 1818) from Fiji, while Djajasasmita and Budiman (1984) have presented some information on the population density of this species in the Pisang River, Sumatra.

The anatomy of this little known bivalve has not been studied. This investigaton helps to remedy this situation but also points out some interesting behavioural adaptations that, linked with anatomical modifications, provides clues as to how the colonisation of freshwaters by this important group of bivalves has been achieved.

MATERIALS AND METHODS

Market specimens of *Batissa violacea* (60 - 90 mm shell length) were first examined alive in Fiji and then subsequently in Hong Kong. Following dissection, ciliary currents were elucidated using fine carborundum and carmine. For histological purposes, two specimens were removed from their valves and fixed in aqueous Bouin's fluid and, following routine procedures, serially sectioned at 6 μm and alternate slides stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

BIOLOGY

Batissa violacea is a tropical freshwater corbiculid distributed throughout the western Pacific, i.e. Malaysia,

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Philippines, New Guinea, N.W. Australia and various Pacific islands. Bentham-Jutting (1953) records it as the only species from Java and from New Guinea (Bentham-Jutting, 1963); Hadl (1976) records it from Fiji; McMichael (1967) from northwestern Australia. Brandt (1974) records *B. similis* Prime, 1860 from the Nicobar Islands and rivers in Thailand.

Raj and Fergusson (1980) reported upon the osmolarity (64.1 ± 8 m Osmol) and ionic composition of the blood of *Batissa violacea* (Na^+, 3.5; K^+, 8.98; Ca^{2+}, 2.98; Mg^{2+}, 26.08; Cl^-, 4.26 mmol kg^{-1} water) and showed them to be comparable to the better-known unionids *Anodonta cygnea* Linnaeus (42 m Osmol; Na^+, 5.3; K^+, 21.3; Ca^{2+}, 12.0; Mg^{2+}, 4.5; Cl^-, 2.4 mmol kg^{-1} water) and *Hyridella menziesi* Gray (62 ± 15 m Osmol; Na^+, 1.6; K^+, 7.2; Ca^{2+}, 2.0; Cl^-, 13.7 mmol kg^{-1} water). They concluded that *B. violacea* is the result of a relatively recent immigration into fresh waters by the Corbiculidae, a view upheld by this author (Morton, 1985; 1987b). Djajasasmita and Budiman (1984) demonstrates that the species occurs in the muds of the banks and river beds in Indonesia.

Eight specimens of *Batissa violacea* obtained alive from Fiji were placed into a freshwater aquarium at 21ºC in Hong Kong, with 15 cm depth of sand. They burrowed rapidly to the full depth. This was thought to be a possible response to perceived drying. Subsequently, two individuals took up residence at the sand water interface, only the tips of their shells above it with the siphons projecting from between the valve margins only slightly. Six other specimens, however, remained buried to a depth of ~ 10 cm from the posterior edge of the shell and even with periodic removal, returned to this depth.

FUNCTIONAL MORPHOLOGY

SHELL

The shell of *Batissa violacea* is equivalve and approximately equilateral, although the posterior is somewhat elongated in relation to the anterior (Fig. 1A). The outline varies considerably, some shells being more rounded, others elongated. A maximum length of 150 mm has been recorded (Bentham-Jutting, 1953). The periostracum is thick and dark; younger shells appear dark violet, older ones black. The older parts of the shell, around the umbones, are often eroded. The opisthodetic external ligament is large. The posterior margin is sometimes square and an umbonal ridge extends to its postero-ventral border much as in *Polymesoda erosa* (Morton, 1976). Seen from the anterior, the shell is narrow, the widest region, as in most burrowers, being dorsal to the mid point of the dorso-ventral axis of the shell (Fig. 1B: x-x). The shell margin gapes anteriorly (Fig. 1B).

The nacreous internal surface of the shell is varying shades of purple, particularly external to the pallial line. This is recessed deeply from within the shell margin and is double, being composed of an inner and an outer line [Fig. 2: PL(I), PL(O)]. The latter is much thicker than the former. Posteriorly, there is a shallow pallial sinus (PS). The anterior and posterior adductor muscles (AA, PA) are deeply impressed into the shell of older individuals, just below the large hinge plate.

The massive external ligament comprises a posterior outer ligament layer (POL) and an inner ligament layer (IL) (Yonge, 1978); if there is an anterior outer ligament layer it is either lost or very reduced. The ligament is overlain by periostracum (PE), extending beyond the ligament as a thick wad that covers the shell and darkens the inner margin of each valve.

The hinge plate (Fig. 3) is broad and the left valve possesses three cardinal teeth (CT), posteriorly directed. These interlock with two teeth in the right valve. The central cardinal tooth of the right valve can be bifid. The left valve has anterior and slightly longer posterior lateral teeth (LT) that fit into sockets on the right valve (LTS). The lateral teeth of the left valve and the lower lips of the sockets of the right valve are grooved transversely.

ADDUCTOR MUSCLES

Batissa violacea is approximately isomyarian, the two adductors being located under the ends of the hinge plate (Fig. 2: AA, PA). Also under each hinge plate beneath the lateral teeth and internal to each adductor is a pedal retractor muscle (APR, PPR). The adductor muscles are divided

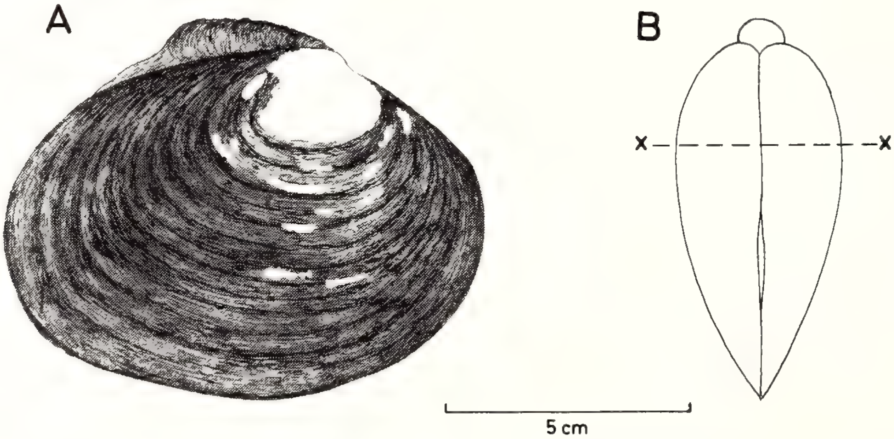

Fig. 1. *Batissa violacea.* The shell as seen from A, the right side and B, from the anterior, showing (x--x) the maximum width.

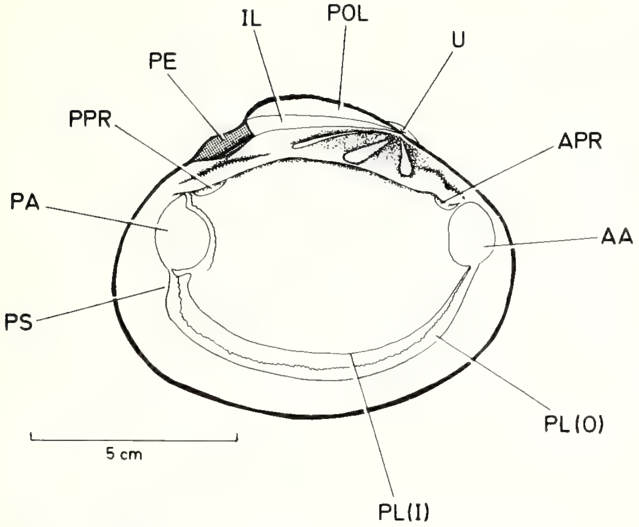

Fig. 2. *Batissa violacea.* An internal view of the left shell valve. [AA, anterior adductor muscle scar; APR, anterior pedal retractor muscle scar; IL, inner ligament layer; PA, posterior adductor muscle scar; PE, periostracum; PL(I), inner component of the pallial line; PL(O), outer component of the pallial line; POL, posterior outer ligament layer; PPR, posterior pedal retractor muscle scar; PS, pallial sinus; U, umbo].

into slow and quick components of smooth and striated muscle bundles.

SIPHONS

The siphons (Fig. 4) are located posteriorly, the exhalant (ES) being small and fringed apically by small papillae. The inhalant (IS) is larger and crowned by a complex array of papillae. There are usually 24 large primary papillae, interspersed by an equal number of smaller secondary papillae. These are interspersed by some 48 tertiary papillae and these, in turn, by approximately 96 tiny quaternary papillae. The siphonal apparatus is thus well endowed with sensory papillae and the shallowness of the pallial sinus attests to the fact that the siphons can extend only slightly from between the shell valves. The siphons are dark brown and flecked with yellow. The inner reaches of the exhalant siphon are yellow. The siphons are formed by fusion of the inner mantle folds only and are thus of type A (Yonge, 1957, 1982). Papillae around the base of the siphons extend dorsally and ventrally as gradually merging and diminishing rows, the latter towards the pedal gape (PG).

MANTLE MARGIN

The mantle margin comprises the usual three folds (Fig. 5), except that the inner fold is divided into two components: inner [IMF(I)] and outer [IMF(O)]. The inner component contains the groove of a major rejectory tract (RT), the outer component has sensory papillae. The inner fold contains the inner component of the pallial retractor muscle [PRM(I)], arising from the inner pallial line [Fig. 2: PL(I)] and constituting the major muscles of the mantle margin where left and right lobes fuse, i.e. between inhalant and exhalant siphons and inhalant siphon and pedal gape. The inner fold contains a few, basiphilic sub-epithelial, mucous cells. The middle fold (MMF) is relatively small and forms the surface against which the periostracum (P) is secreted from the inner surface of the outer fold. The larger outer component of the pallial retractor muscle [PRM(O)], arising from the outer component of the pallial line [Fig. 2: PL(O)], is closely associated with the periostracal groove. The outer mantle fold (OMF) is large and contains a haemocoel. There is a pallial nerve (PN) between inner and outer components of the pallial retractor muscle.

PEDAL GAPE

The anterior pedal gape (Fig. 6: PG) is long, the inner folds forming it being extensively equipped with blunt-tipped papillae. These are larger at the posterior and anterior extremities of the pedal gape. Anteriorly too, the shell is emarginated (Fig. 1B) and water is forcibly expelled here when the animal is handled.

CTENIDIA

The ctenidia are flat, homorhabdic, eulamellibranch and plicate. Each plica comprises up to 48 filaments. Each ctenidium comprises inner and outer demibranchs (Fig. 6A: ID, OD), the latter dorsoventrally much shorter than the former.

The ctenidia are relatively small occupying, approximately, the postero-dorsal quadrant of the mantle cavity. The ctenidial ciliation is of type C(2) (Atkins, 1937a) (Fig. 6B), also seen in *Polymesoda erosa* (Morton, 1976). Acceptance tracts are thus located in the ventral marginal food grooves of both demibranchs and in the ctenidial axis, but not in the junctions created by the ascending lamellae of the inner and outer demibranchs with the visceral mass and mantle respectively. The

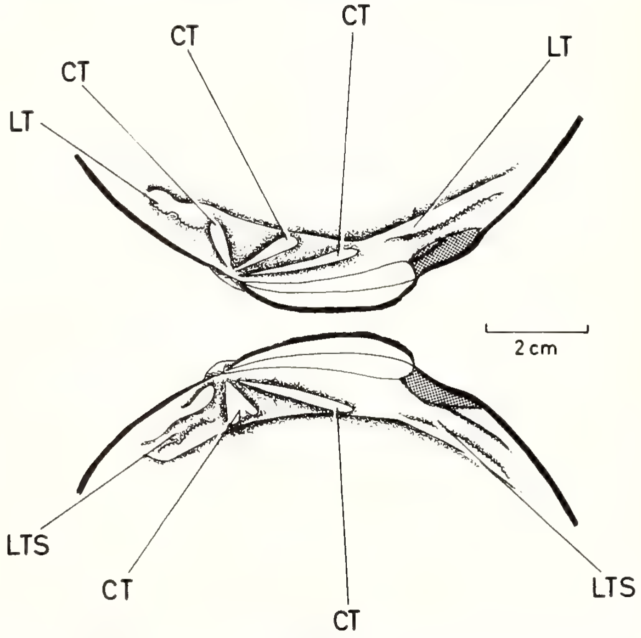

Fig. 3. *Batissa violacea.* The hinge plate, left valve above, right below (CT, cardinal tooth; LT, lateral tooth; LTS, lateral tooth socket).

edges of the ascending lamellae of both inner and outer demibranchs are connected to the visceral mass and mantle respectively by tissue fusions (Atkins, 1937b).

LABIAL PALPS

The labial palps (Fig. 6: LP) are large and their posterior edges are associated closely with the ventral marginal food grooves of the ctenidia. The ctenidial-labial palp junction is of Category 3 (Stasek, 1963). Thus, material arriving at the ctenidial termini move on to a short distal oral groove, but is probably collected from the ventral food grooves by the general palp surfaces before reaching this point.

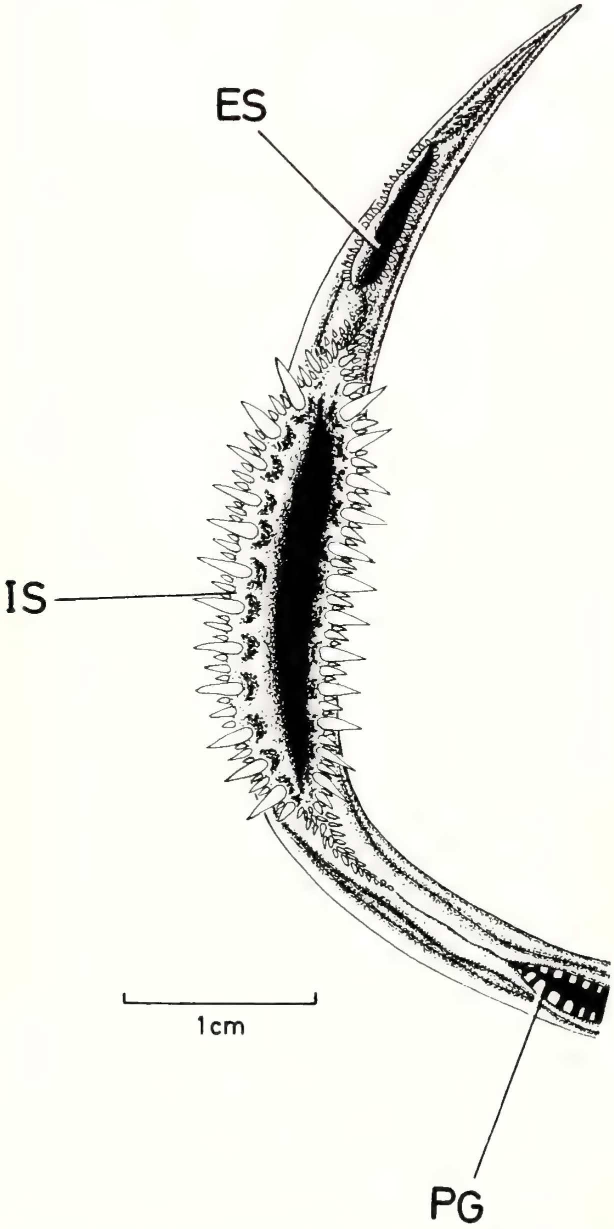

Fig. 4. *Batissa violacea:* The posterior shell margin showing the siphons (ES, exhalant siphon; IS, inhalant siphon; PG, pedal gape).

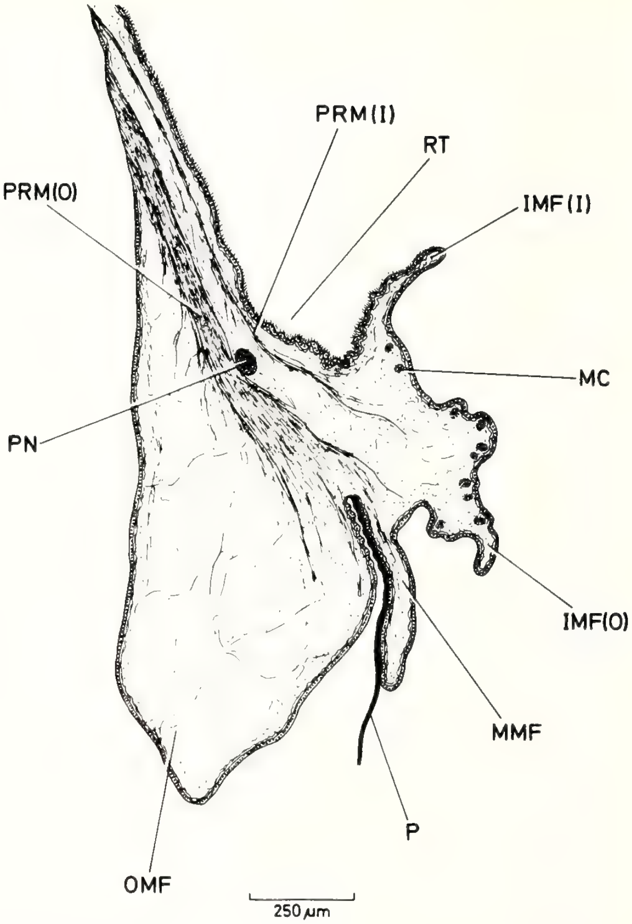

Fig. 5. *Batissa violacea.* A transverse section through the right mantle lobe at the pedal gape [IMF(I), inner component of the inner mantle fold; IMF(O), outer component of the inner mantle fold; MC, mucous cell; MMF, middle mantle fold; OMF, outer mantle fold; P, periostracum; PN, pallial nerve; PRM(I), inner component of the pallial retractor muscle; PRM(O), outer component of the pallial retractor muscle; RT, rejectory tract].

The detailed ciliary currents of two palp ridges and an intervening groove are shown in figure 7. Fine, accepted particles are transported rapidly over the surface of the palps to the distal oral groove and thence via a short proximal oral groove to the mouth, located ventral to the anterior pedal retractor muscle. Large, unwanted particles fall into the depths of the groove and are transported towards the ventral edge of the palp where they then pass to its free tip and are rejected. On the oral and aboral faces of the palp ridges are complex re-sorting currents that allow *Batissa violacea* to accept or reject intermediate-sized particles in greater or lesser quantities.

CILIARY CURRENTS OF THE VISCERAL MASS AND MANTLE

The ciliary currents of the visceral mass are shown in figure 6. At the approximate junction of the foot (F) with the

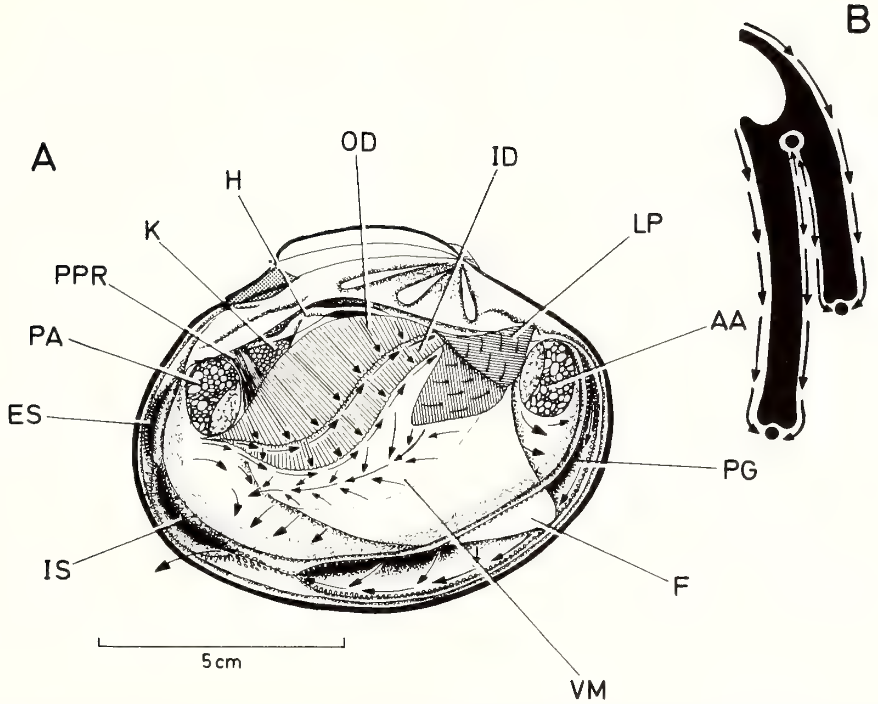

Fig. 6. *Batissa violacea.* A, The animal as seen from the right side and after removal of the right shell valve and mantle lobe. Ciliary currents are indicated by arrows; B, a diagrammatic transverse section through a single ctenidium showing the ciliary currents and acceptance tracts (•). (AA, anterior adductor muscle; ES, exhalant siphon; F, foot; H, heart; ID, inner demibranch; IS, inhalant siphon; K, kidney; LP, labial palp; OD, outer demibranch; PA, posterior adductor muscle; PG, pedal gape; PPR, posterior pedal retractor muscle; VM, visceral mass).

visceral mass (VM), a rejectory tract extends along each side from the position of the palp tip to the posterior edge of the visceral mass. These tracts are fed from above by downward cleansing currents and from below by cilia collecting material from the dorsal regions of the foot. The foot itself is free of such cleansing cilia. Material collected in the left and right grooves eventually falls onto the mantle below.

The ciliary currents of the mantle complement those of the visceral mass. Each lobe possesses a deep rejection tract formed at the junction of the inner component of the inner mantle fold with the general mantle surface. Unwanted material from the general mantle surface is passed downwards into the left and right rejectory tracts and transported towards the base of the inhalant siphon where it is rejected as pseudofaeces (Fig. 6).

ORGANS OF THE PERICARDIUM

The heart (Fig. 8) lies beneath the ligament. It comprises a single ventricle (V) penetrated by the rectum (R), and a pair of auricles (AU). From the posteroventral edge of the pericardium arise a pair of renopericardial apertures (RPA) that open into the distal limbs of the kidneys (K). The kidneys are located between the pericardium and the posterior adductor muscle (PA). The rectum passes above them. The proximal limbs of the kidneys open into the suprabranchial chamber, as renal apertures (RA), between the ctenidial axis and the point of attachment of the ascending lamella of the inner demibranch to the visceral mass (PALID). Located close

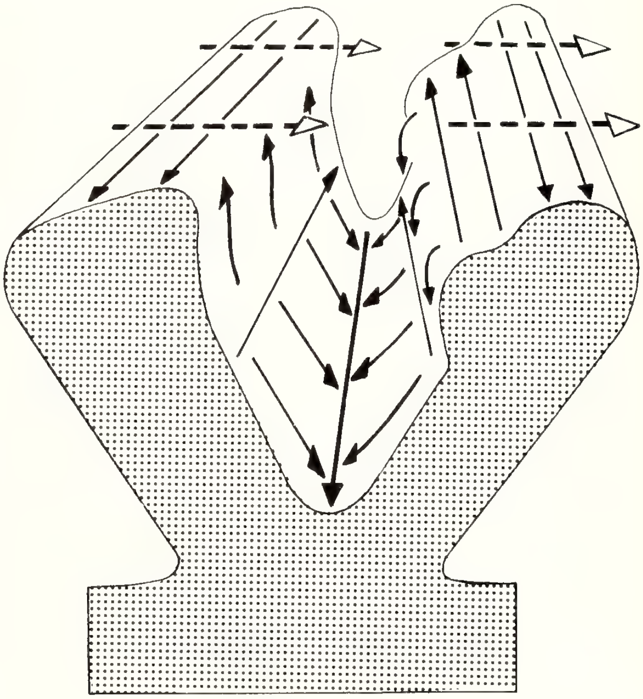

Fig. 7. *Batissa violacea.* A diagrammatic representation of two ridges of a labial palp to show the various ciliary tracts (for explanation see text).

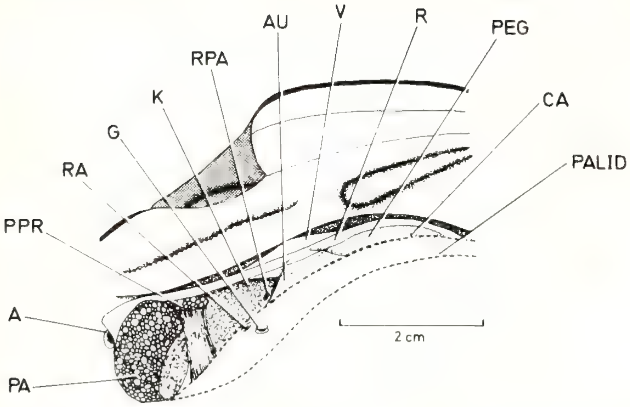

Fig. 8. *Batissa violacea.* The organs of the pericardium as seen from the right side. (A, anus; AU, auricle; CA, ctenidial axis; G, gonopore; K, kidney; PA, posterior adductor muscle; PALID, point of attachment of ascending lamella of the inner demibranch to the visceral mass; PEG, pericardial gland; PPR, posterior pedal retractor muscle; R, rectum; RA, renal aperture; RPA, renopericardial aperture; V, ventricle).

to the renal apertures are the gonopores (G). *Batissa violacea* is dioecious. Eggs shed in the laboratory measured between 80-120 μm. The pericardial gland (PEG) is largely associated with the anterior pericardium (White, 1942) as in *Polymesoda (Geloina) erosa* (Morton, 1976).

DISCUSSION

On first inspection, the black shell of *Batissa violacea* is strongly reminiscent of riverine Unionidae (see illustrations in Burch, 1975) and indeed this species, among the Corbiculidae, is a tropical riverine species (Djajasasmita and Budiman, 1984). The similarity in shell form can be regarded as an example of convergent evolution.

In other aspects of its anatomy, however, *Batissa violacea* is a typical corbiculid, similar in most respects to *Polymesoda (Geloina) erosa* (Morton, 1976). An important feature of the latter species is that the pallial line is single, whereas in *B. violacea* it is double. The condition in *Batissa* stems from duplication of the inner mantle fold and a close association between the outer pallial retractor component with the periostracal groove. The periostracum of *B. violacea* is thick, and could have an important protective function for the shell in acidic, tropical waters.

A further important feature of the *Batissa violacea* shell is the anterior gape through which water is ejected when the animal is handled. This is also seen in *Polymesoda erosa*, which has been shown to feed from subterranean water (Morton, 1976). This probably also occurs in *B. violacea*, and it is perhaps significant that this species is capable of living deep within the sediment with no siphonal access to the substratum surface. The posterior margin of the shell would generally be located at the sediment-water interface but in times of drought the species can probably dig deeper into the sediment and effect simple exchange with the water table via the pedal gape. It is interesting to note that Sinclair and Isom (1963) illustrate *Corbicula fluminea* as capable of living in deep, moist, sediments. Indeed, the species has been dug up alive from sands with little evidence of flowing water, and has been found to cause problems subsequently in concrete aggregates.

McMahon (1983) has reviewed mechanisms of desiccation tolerance in *Corbicula fluminea* and shown that aerial respiration is possible for a period of a few days (McMahon, 1979) at the posterior mantle margin, as in *Polymesoda erosa* and *P. proxima* (= *P. expansa*) (Morton, 1975, 1976, 1984). With the corbiculid capacity for pedal gape feeding and the potential for deep residence, it would seem that the first response to surface drying is to dig to deeper moisture levels. Highly stressed *C. fluminea*, however, crawl to the surface and are washed downstream (McMahon, 1983). Prezant and Chalermwat (1984) report that *C. fluminea* produces mucous drogue lines that facilitate downstream floatation. The first facility could be important in the relatively recent colonisation of freshwaters by the Corbiculidae, the latter two particular behaviours expressed under conditions of stress by *C. fluminea*, a head-water and lentic species. Derived from a marine ancestor (Raj and Fergusson, 1980; Morton, 1987b), modern representatives of the Corbiculidae have had to withstand periodic drought, either tidal in *Polymesoda* (Morton, 1976) or seasonal as in *Batissa* and *Corbicula*. The mechanism to overcome drought now demonstrated for *Batissa* as well as *Polymesoda* points to an important behavioural adaptation that has facilitated colonization of first estuarine and then lacustrine habitats.

In all other respects, the Corbiculidae are little different morphologically from other Veneroida. Like *Polymesoda* (Morton, 1985), *Batissa* is dioecious and non-incubatory and, with a maximum shell length of 150 mm and numerous growth lines (Bentham-Jutting, 1953), probably long-lived. The osmolarity and ionic composition of *Batissa* blood indicates recent colonisation of freshwaters (Raj and Fergusson, 1980). A simple morphology and reproductive strategy are also suggestive of this. Thus, physiological specializations and behavioural adaptations to avoid drought were critical for the exploitation of freshwaters particularly the lower reaches of rivers. Later reproductive specialisations, i.e. a variable sex ratio and incidence of hermaphroditism, as in *Corbicula flumina*, allowed colonisation of river head waters and lentic systems, with reductions in size and longevity (Morton, 1987b). Behavioural specialisations to avoid drought (McMahon, 1983) were, however, important in the progressive colonisation of fresh waters by the Corbiculidae.

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BIVALVES IN THE GENUS *CORBICULA* (BIVALVIA: CORBICULIDAE) IN THE SOVIET UNION WITH A CATALOGUE OF TYPE MATERIALS IN THE ZOOLOGICAL INSTITUTE, ACADEMY OF SCIENCES OF THE U.S.S.R., LENINGRAD

CLEMENT L. COUNTS, III
COASTAL ECOLOGY RESEARCH LABORATORY
UNIVERSITY OF MARYLAND EASTERN SHORE
PRINCESS ANNE, MARYLAND 21853, U.S.A.

ABSTRACT

Type materials for three species and three subspecies of bivalves in the genus *Corbicula* held in the collections of the Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad, are reported. Catalogue numbers, number and type of specimens, locality data from collection labels, and dates of collection are provided for 39 lots of type materials for *C. ferghanensis, C. fluminea extrema, C. fluminea praebaicalensis, C. lindholmi, C. suifuensis* and *C. suifuensis finitima.* Notes on other species of fossil and Recent *Corbicula* described from the U.S.S.R. are given with a discussion of their zoogeography. The debate on the number of species of *Corbicula* within the Soviet Union is discussed with a review of current practices used to resolve this systematic problem.

Bivalves in the genus *Corbicula* Mühlfeldt, 1811, have been the object of malacological study in the Soviet Union for many years. While some research on the morphology, physiology and ecology of corbiculids has been conducted by Soviet malacologists (Mitropolskie, 1963; Butenko, 1967; Sultanov *et al.*, 1972; Kasymov and Gadshiyeva, 1974; Alimov, 1974, 1975; Karpevich, 1975; Yaroslavteva *et al.,* 1981; Zaiko and Romanenko, 1981; Komendantov, 1984), most reports on Soviet corbiculids concern their paleontology (Androussov, 1923; Slokedewitsch, 1938; Otatume, 1943; Suzuki, 1943; Volkova, 1962; Andrusov, 1966; Krylova, 1966; Yakushima, 1968, 1973; Zhubkova *et al.,* 1968; Ibadov, 1972; Dubinovs'kyi *et al.,* 1974; Khubka, 1979). This is not so surprising since most Soviet malacologists are trained as geologists with an emphasis on stratigraphy and paleontology (Amitrov, 1983; Counts, 1986). There have also been some reports on the biogeography of bivalves in the genus *Corbicula* within the Soviet Union (Rosen, 1914; Sidaroff, 1929; Decksbach, 1943; Zhadin, 1952; Aliev, 1960; Volkova, 1962; Mitropolskie, 1963; Kasymov, 1972; Kasymov and Gadshiyeva, 1974; Karpevich, 1975; Izzatullaev, 1980; Izzatullaev and Starobogatov, 1985). Two recent reviews of the systematics of genus *Corbicula* in the Soviet Union have appeared (Kursalova and Starobogatov, 1971; Izzatullaev, 1980), one of which (Kursalova and Starobogatov, 1971) included descriptions of new taxa.

Several species and subspecies of recent and fossil bivalves in the genus *Corbicula* have been described from Soviet waters over the past century (von Martens, 1874; Clessin, 1879; Androussov, 1923; Lindholm, 1927; Slokedewitsch, 1938; Otatume, 1943; Suzuki, 1943; Popova, 1968; Yakushima, 1968; Zhubkova *et al.,* 1968; Kursalova and Starobogatov, 1971). The type materials of three species and three subspecies are located in the collections of the Zoological Institute, Academy of Sciences of the U.S.S.R., Leningrad. This paper discusses the species of bivalves in the genus *Corbicula* in the Soviet Union and presents notes on the type materials held in the Zoological Institute's collections.

TYPE MATERIALS

A survey of the corbiculid materials in the collections of the Zoological Institute of the Academy of Sciences of the U.S.S.R., Leningrad, was made during April 3 - 16, 1986. Due to the institutional practice of providing only lots selected from the card catalogue, it was not possible to examine the entire collection in the ranges.

The type material for three species and three subspecies of bivalves in the genus *Corbicula* now in the collections of the Zoological Institute of the Academy of Sciences of the U.S.S.R., Leningrad (AH-CCCP) are presented below. All of these species were described from Soviet waters. It should be noted that the rules for designation of type specimens and localities are somewhat more flexible among Soviet malacologists than among their western colleagues.

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In some instances, specimens designated as paratypes are from localities other than the holotype or syntypes. Further, some paratype series were collected over a period of 40 years. While these idiosyncracies are not unique to materials in the collections of the AH-CCCP, they do apply to all the type materials referred to the genus *Corbicula* in that institution.

None of the type materials discussed below were designated by lot number in the literature that describes them with the exception of the holotype of *Corbicula fluminalis praebaicalensis* (Popova, 1968). Taxa, catalogue numbers, number of specimens, type localities, and dates of collection are provided below.

Corbicula ferghanensis Kursalova and Starobogatov, 1971, p. 95 (Uzbek S.S.R., Aral Sea Region, Ferghana River).

AH-CCCP 446-1961, No. 1, Holotype, Ferghana (River), 4 IV 1931. Collected dead.

AH-CCCP 446-1961, No. 2, 10 + 1/2 paratypes, dry, Ferghana (River), 4 IV 1931. Collected dead.

AH-CCCP 446-1961, No. 3, 2 + 6/2 paratypes, dry, Ferghana (River), 1931.

AH-CCCP 446-1961, No. 4, 8 paratypes, dry, Ferghana (River), near (power?) station, 13 IV 1931.

AH-CCCP 446-1961, No. 5, 2/2 paratypes, dry, Karakalpak Autonomous S.S.R., Muynak, 26 VI 1947.

AH-CCCP 41-1964, No. 6, 1 paratype, dry, Farkhskoe Reservoir and tributaries, Tadzhikistan (Tadzhik S.S.R.), 14 VII 1960.

AH-CCCP 41-1964, No. 7, 1 paratype, dry, shallow water, Kairak-Kumskoe Reservoir, Tadzhikistan (Tadzhik S.S.R.), 5 X 1960.

AH-CCCP 41-1964, No. 8, 1 paratype, dry, Kairak-Kumskoe Reservoir, Tadzhikistan (Tadzhik S.S.R.), 30 XI 1960.

AH-CCCP 483-1967, No. 9, 37 + 29/2 paratypes, dry, Right bank of Syr-Dar'ya River, Samgar Canal from Kairak-Kumskoe Reservoir, 25 VII 1967.

AH-CCCP 284, No. 10, 3/2 paratypes, dry, (no locality, no date).

AH-CCCP 284-1969, No. 11, 9/2 paratypes, dry, (no locality), 1968.

AH-CCCP 175-1929, No. 12, 1/2 paratype, dry, (no locality), 21-22 IX 1928.

AH-CCCP 241-1962, No. 13, 1/2 paratype, dry, (no locality, no date).

AH-CCCP 359-1935, No. 14, 2/2 paratypes, dry, (no locality, no date).

AH-CCCP 452-1973, No. 15, 4/2 paratypes. Quaternary fossils, (no locality, no dates). The label accompanying these specimens indicates they are also paratypes of *Corbicula fluminea praebaicalensis.*

Remarks: *Corbicula ferghanensis* is also reported from a large irrigation ditch off the Ferghan River near the village of Arkangelisk (Kursalova and Starobogatov, 1971). Izzatullaev (1980) reported *C. ferghanensis* in the Syr Dar'ya basin (Ferghan River) and Amu Dar'ya basin (Karakum and Samarkand) in the Tadzhik and Uzbek S.S.R. He also noted its presence in the environs of lakes Baikal, Irtash, and Balkash.

Corbicula fluminea extrema Lindholm, 1927, 28:550.

AH-CCCP 465-1929, No. 2, 4 syntypes in alcohol, Amur estuary near Dzhaore, 19 VI 1928.

AH-CCCP 198-1961, No. 2, 2 syntypes, dry, Amur estuary near Dzhaore, 19 VI 1928.

AH-CCCP 465-1929, No. 3, 2 + 2/2 syntypes, in alcohol, Osmrov Canal, 18 VIII 1928.

AH-CCCP 465-1929, No. 4, 5 syntypes, dry, Vladimir Bay, Sea of Japan, VIII 1927. (All collected dead with umbones and internal shell features badly eroded).

AH-CCCP 465-1929, No. 5, 1 syntype, dry, Sachalin (Sakhalin) Island near Astrakhanovskii, 12 VII 1928.

AH-CCCP 456-1929, No. 6, 13 syntypes, dry, Amur estuary near Dzhaore, 26 VI 1928.

Remarks: Kursalova and Starobogatov (1971) recognized *Corbicula fluminea extrema (Corbicula fluminalis extrema* in their paper) as a junior synonym of *C. japonica* Prime, 1864. They reported the species to be present in the waters of the continental coast of the Sea of Japan, the Amur River estuary, and the southern Kurile Islands and Sakhalin Island, as well as Japan.

Corbicula fluminea praebaicalenis Popova, 1968, pp. 257-258, Pl. 1, Figs. 13-15 (northwest Prebaikal, River Anga).

AH-CCCP 452-1973, No. 1, 22 /2 paratypes, Quaternary fossils, (no locality, no date).

AH-CCCP 452-1973, No. 2, 4/2 paratypes, Quaternary fossils, (no locality, no date). Reidentified as *Corbicula ferghanensis* (AH-CCCP 452-1973, No. 16).

Remarks: The holotype of *Corbicula fluminea praebaicalensis* is located in the collection of the Limnological Institute, Academy of Sciences of the U.S.S.R., Irkutsk (No. 20/64A) (designated by Popova, 1968). Kursalova and Starobogatov (1971) report the taxon to be a junior synonym of *C. tibetensis* (Prashad, 1929).

Corbicula lindholmi Kursalova and Starobogatov, 1971, p. 94.

AH-CCCP 205, 1938, No. 1, Holotype, Ussuri River, Suifun River (23-25 VII 1924).

AH-CCCP 460-1929, No. 2, 1 paratype in alcohol, Suifun River and its estuary, 20 VII 1925.

AH-CCCP 198-1961, No. 3, 2 paratypes, dry, Suifun River, 18 VIII 1928. (Three specimens are listed on the label but only two specimens are in the lot. Both were collected dead and show erosion of the internal shell features, especially the lateral teeth.)

AH-CCCP 198-1961, No. 4, 1 paratype, dry, Suifin River, 1925.

AH-CCCP 212-1925, No. 5, 1 paratype, dry, (no locality), 1925.

Remarks: Kursalova and Starobogatov (1971) also report *Corbicula lindholmi* from the South Primorie and upper portion of the Sungari River basin, the lower portion of the Pauecheza River near the villages of Dulakeet and Derzharena. They noted specimens were cast ashore on Slavyank Creek (also known as Velik Creek) at Razina. They also report populations near the frontier of the People's Republic of China at the village of Velikovsk.

Corbicula suifuensis Lindholm, 1925, p. 29; 1927, Pl. 32, Figs. 1a, 1b (Suifun River near Razhdolnaya, southeastern Siberia).

AH-CCCP 216-1924, Holotype, dry, Suifun River, VII 1924.
AH-CCCP 216-1924, No. 2, 1 paratype, dry, Suifun River, VII 1924.
AH-CCCP 205-1938, No. 3, 3 paratypes, dry, Suifun River, 23-25 VII 1942.
AH-CCCP 205-1938, No. 4, 1 paratype, dry, Suifun River, VII 1924 ("*C. producta*" is written on the valves).
AH-CCCP 460-1929, No. 6, 1 paratype, dry, Suifun River and its estuary, Primorie region, (no date).
AH-CCCP 460-1929, No. 7, 1 paratype, dry, Suifun River and its estuary, Primorie region, (no date).
AH-CCCP 460-1929, No. 8, 1 paratype, dry, Suifun River and its estuary, Primorie region, (no date).
AH-CCCP 460-1929, No. 9, 1 paratype, dry, Suifun River and its estuary, Primorie region, (no date).
AH-CCCP 460-1929, No. 10, 7 paratypes, dry, Suifun River and its estuary, Primorie region, (no date).

Remarks: Other records are the River Maikhe, coast of Posaeta Bay, Primorie (Kursalova and Starobogatov, 1971).

Corbicula suifuensis finitima Lindholm, 1927, pp. 553-554, Pl. 32, Figs. 2a, 2b (Estuary of the Mai-che River, southeastern Siberia).

AH-CCCP 460-1929, No. 1, Holotype, dry, rivers and estuaries of the Primorie region, (no date).
AH-CCCP 460-1929, No. 2, 2 paratypes, dry, rivers and estuaries of the Primorie region, 24 VI 1924.

Remarks: Kursalova and Starobogatov (1971) report *Corbicula suifuensis finitima* to be a junior synonym of *C. elatior* Martens, 1905.

DISCUSSION

Other bivalve taxa described from waters of the Soviet Union have been referred to the genus *Corbicula*. Clessin (1879) described *C. hohenackeri* from the Jalysch River of the Caucasus. The type materials for this species were in the Stuttgart Museum and are believed to have been destroyed during World War II. Martens (1874) described *C. minima* from Samarkand and Lindholm (1933) later reported collecting the species in Central Asia. The type materials for the species was believed to be in the collections of the Zoological Museum in Moscow. However, all attempts by Soviet malacologists to locate these materials have failed and the types are now considered lost (Starobogatov, pers. comm., 1986).

Several fossil species have been described from strata in the Soviet Union. Androussov (1923) described *Corbicula fluminalis apscheronica* from the Pleistocene of the Apscheron Peninsula, Azerbaidzhan. *C. fonsata* and *C. kovatschensis* were described from the Soviet Union Far East (Slokedewitsch, 1938). Many fossil species have been described from the strata of Sakhalin Island. These include *C. sakakibarai* Otatume, 1943 from the Naibuchi Group, south Sakhalin Island; *C. gabliana lautenschlageri* Zhubkova *et al.*, 1968 described from the Pliocene of the River Tym; *C. matachiensis* Zhubkova *et al.*, 1968 from the upper Miocene-Pliocene of the River Mach; and *C. glabiana adamensis* described from the upper Miocene-Pliocene of Sakhalin Island. Further south, Yakushima (1968) described *C. susaensis* from the upper Cretaceous of the south Primorye. My efforts to locate type material for these taxa have not been successful. However, type materials for two fossil taxa are presently in the collection of the Institute of Geology and Paleontology (IGPS) of the University of Tokyo: *C. shimizui* Suzuki, 1943 (Holotype IGPS 8353b, Paratype IGPS 8353a) and *C. sachalinensis* Suzuki, 1943 (Holotype and Paratypes IGPS 8353a); both species from the Tertiary Aquitanian Mach Group of the middle course of the Tumis River, North Sakhalin Island.

Corbicula fluminalis (Müller, 1774) appears to be the most widely distributed species within the Soviet Union. This is reflected both in published accounts and in the collections of the AH-CCCP in so far as I was able to examine them. *C. fluminalis* has been generally reported from the Caucasus in Azerbaidzhan, Iran, Syria, Afghanistan, India, Soviet Central Asia, and Baluchistan (Kasymov, 1972). Likharev and Starobogatov (1967) and Solem (1979) have also reported *C. fluminalis* from Afghanistan. Lindholm (1930) reported *C. fluminalis* from Buchara (now Uzbek S.S.R.). Decksbach (1943) reported *C. fluminalis* from Azerbaidzhan and Kazakhistan. He also reported the species in Uzbekistan at the mouth of the Amu Dar'ya River and in the Amur Basin. He further noted its presence in Turkmenia in the valley of the Murgrab River. Zhadin (1952) reported *C. fluminalis* to be distributed throughout the bays of the southern Caspian Sea, the Transcaucasus (Kura River basin and Lake Adzhikabul), in the irrigation canals of Ashkabad and the lower reaches and delta of the Amu Dar'ya at Samarkand, as well as the Murgab River. He further noted that *C. fluminalis* are found as fossils in Quaternary strata in the Moldavian S.S.R. (Dniester Terraces), the Ukranian S.S.R., and in the Pleistocene Apscheron Layer of the Betekei River, western Siberia. Volkova (1962) reported *C. fluminalis* from the lower reaches of the Irtysh River. Kursalova and Starobogatov (1971) reported the species in the Azerbaidzhan and Turkmen S.S.R. and in the Amu Dar'ia. This may be the species referred to by Sidaroff (1929) in the Aral Sea. Boettger (1881) reported the subspecies *C. fluminalis crassula* 'Mousson' Bellardi, 1854 and *C. fluminalis compressa* 'Mousson' Deshayes, 1854 from Lake Adzhikabul, Transcaucasus (Azerbaidzhan S.S.R.).

Corbicula japonica Prime, 1864, is also reported to be widely distributed in the Soviet Far East. This, again, is reflected in both published accounts and in the records of the AH-CCCP. *C. japonica* is variously reported from the Razhdolnaya River (Zaiko and Romanenko, 1981) and from the brackish water reaches of the Amur River estuary and from Dzhaore Cape, Uarke Cape, the Chastye Islands of Sakhalin Island, and in the northwestern part of the estuary at Schatije Bay and Khalesovo Cape (Garkalina and Moskvicheva, 1984). Kursalova and Starobogatov (1971) note that *C. japonica* is widespread throughout the continental estuaries of the Sea of Japan, the Amur estuary, Sakhalin

Island, and the Kurile Islands. Other records for *C. japonica* in Soviet waters from AH-CCCP include: Sakhalin Island on a coastal spit near Nabil; Lake Ain, Sakhalin Island; Sugan River Bay; Amurskiy Bay near Ussi; the Sea of Okhotsk, Sakhalin Zaliv, and the northern limits of Amurskiy Bay.

Soviet malacologists are debating the number of species referable to the genus *Corbicula* within the Soviet Union (Kasymov, 1972; Izzatullaev, 1980; Izzatullaev and Starobogatov, 1985). These arguments take on many of the features of the same debate occurring in North America concerning the number of species of corbiculids in that continent (Britton and Morton, 1979, 1986; Hillis and Patton, 1980; McLeod and Sailstad, 1981; McLeod, 1986; Morton, 1987). In the United States, this debate has been resolved to the satisfaction of most malacologists by the use of biochemical genetic techniques (although there now appears to be a debate about whether there is a debate). Soviet malacologists are attempting to resolve their problems using morphological, ecological, and reproductive characteristics (Izzatullaev, 1980).

Kursalova and Starobogatov (1971) reported fourteen species of *Corbicula* within north and west Asia and Europe. These were *C. japonica, C. elatior, C. producta* Martens, 1905, *C. finitima, C. lindholmi, C. fluminalis, C. cor* (Lamarck, 1818), *C. consobrina* (Caillaud, 1826), *C. delessertiana* Prime, 1870, *C. pusilla* (Philippi, 1846), *C. purpurea* Prime, 1864, *C. hebraica* Locard, 1883, *C. tibetensis,* and *C. ferghanensis.* These species were identified on the basis of shell characters with particular emphasis on tooth morphology.

Izzatullaev (1980) identified five species of corbiculid bivalves from the Central Asian republics on the basis of their reproductive biology. These included *Corbicula cor, C. fluminalis,* and *C. purpurea* which were reported to be oviparous. *C. tibetensis* and *C. ferghanensis* were referred to the Australian genus *Corbiculina* Dall, 1903 on the basis of their ovoviviparity.

Soviet malacologists regard the curvature (or degree of inflation) of the shell (Logvinenko and Starobogatov, 1971) as an important systematic tool in identifying their corbiculid species (e.g. Izzatullaev, 1980). The method involves tracing the curvature of a valve using a *camera lucida* and matching the resulting curve to other specimens. It should be noted that this method does not stand as a single test for taxon assignment and that other shell characters are used. However, my experience indicated that the shell curvature method was used in many cases as the critical determining factor in referring corbiculids to taxa in the Soviet Union. The most troublesome aspect of depending upon the shell curvature is that it does not take into account the physical and biological factors that can affect interpopulation differences in shell growth rates and hence, affect the degree of shell inflation.

For example, specimens of *Corbicula fluminea* in the collections of the Delaware Museum of Natural History (DMNH 110469) and Texas Christian University (TCU 6087) from unnamed irrigation ditches at Montezuma's Well National Monument, Yavapai County, Arizona, demonstrate extreme lateral compression of the valves. Yet, this condition is regarded as an expression of response to environmental conditions rather than indicative of another species (Britton and Morton, 1986). Prezant and Chalermwat found that shell microstructure (1983) and internal shell color changes (1983, 1984) could be induced in *C. fluminea* by alteration of the thermal and trophic regimes. While color change could be induced only from purple to white, Prezant and Chalermwat speculated that many of the morphological differences seen in North American corbiculids could be a reflection of microhabitat rather than species-specific differences.

Britton and Morton (1986) and Morton (1987) further noted the polymorphism among populations of *Corbicula fluminea* in North America and Hong Kong, respectively. These studies report differences in shell morphology and color on the basis of sex as well as differences in water quality. Morton (1987) particularly noted that pH, dissolved oxygen and carbon dioxide, and potassium were highly correlated with morphological differences in *C. fluminea* of Hong Kong. Britton and Morton (1986) found that shell characters were unreliable to differentiate between the color morphs of *C. fluminea* North America. On the basis of this and other ecological data, they concluded that there was only one species of *Corbicula* in North America. These considerations are not addressed in any detail by Soviet malacologists with respect to species determination. As yet, no malacologist in the U.S.S.R. has attempted to resolve systematic problems within the genus *Corbicula* using electrophoretic techniques.

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FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1987

ASSETS			
Current Assets			
AMU Operating Acct#3400934	$19,070.27		
Fortune Fed./C.D. #0203206756	3,764.62		
Fortune Fed./C.D. #0203206757	2,444.38		
Fortune Fed./C.D. #0203127749	5,850.09		
Fortune Fed./C.D. #0433212265	21,095,41		
San Antonio Acct. #680005702	3,345.78		
Amer. Life & Casualty Ins. Co.	13,125.56		
Total Current Assets		$68,696.11	
Other Assets			
Total Other Assets		.00	
Total Assets			$68,696.11
LIABILITIES AND EQUITY			
Current Liabilities			
Total Current Liabilities		.00	
Equity			
Retained Earnings	$61,812.00		
Net Income (Loss)	6,884.11		
Total Equity		$68,696.11	
Total Liabilities and Equity			$68,696.11

RECEIPTS:	Current-Period Amount	Current-Period Ratio	Year-to-Date Amount	Year-to-Date Ratio
Memberships:				
Regular	$ 244.50	6.22	$ 7,550.00	15.41
Life	.00	.00	500.00	1.02
Sustaining	.00	.00	135.00	.28
Student (Regular)	16.50	.42	429.50	.88
Student (Foreign)	.00	.00	93.00	.19
Corresponding	53.50	1.36	1,033.60	2.11
Clubs	.00	.00	694.00	1.42
Institutions	174.00	4.43	2,152.00	4.39
Total Memberships Receipts	$ 488.50	12.43	$12,587.10	25.70
Sales:				
AMB Bulletin/Back Copies	17.00	.43	390.00	.80
AMB Bulletin/Special Edition	.00	.00	6,138.00	12.53
AMB Bulletin/Page Charges	.00	.00	1,207.00	2.46
AMU Bulletin/Reprint	.00	.00	797.00	1.63
How to Study and Collect Shells	.00	.00	164.70	.34
Bulletin Account	.00	.00	5,864.00	11.97
Total Sales Receipts	$ 17.00	.43	$14,560.70	29.73
Other Receipts:				
Endowment Fund Donations	.00	.00	3,197.29	6.52
Interest on All Accounts	3,422.18	87.06	4,703.50	9.60
Miscellaneous Donations	3.00	.08	74.19	.15
AMU Registration/Meeting	.00	.00	12,924.00	26.37
Student/Publish	.00	.00	29.50	.06
Student/Award	.00	.00	615.50	1.26
Reprints	.00	.00	250.00	.51
Special Edition	.00	.00	62.50	.13
Total Other Receipts	$3,425.18	87.14	$21,856.48	44.60
Total Cash Receipts	$3,930.68	100.00	$49,004.28	100.03

	Current-Period Amount	Current-Period Ratio	Year-to-Date Amount	Year-to-Date Ratio
DISBURSEMENTS:				
*AMU Bulletin*Expenses	$ .00	.00	$ 15.00	.03
AMU Bulletin/Postage	.00	.00	196.01	.40
AMU Bulletin/Printing	9,238.62	235.04	19,182.40	39.14
AMU Newsletter/Postage	.00	.00	369.93	.75
AMU Newsletter/Printing	.00	.00	805.33	1.64
AMU Newsletter/Expenses	.00	.00	113.50	.23
Other Postage	.00	.00	379.66	.77
Other Printing	.00	.00	63.87	.13
Office Supplies	.00	.00	185.10	.38
Dues	.00	.00	560.00	1.14
Officer's Travel	.00	.00	2,265.00	4.62
Filing Fee (Calif.)	.00	.00	49.16	.10
Symposium Endowment Fund Dep.	.00	.00	2,000.00	4.08
Student Awards	.00	.00	750.00	1.53
Insurance	.00	.00	231.00	.47
Telephone	.00	.00	22.66	.05
Bank Charges	.00	.00	13.00	.03
Miscellaneous/Petty Cash	.00	.00	431.70	.88
AMU Meeting	.00	.00	14,350.54	29.28
Newsletter Expenses	.00	.00	.52	.02
Membership Committee	.00	.00	135.79	.28
Total Disbursements	$9,238.62	235.04	$42,120.17	85.93
Net Income (Loss)	$5,307.94	135.04	$ 6,884.11	14.10

AMERICAN MALACOLOGICAL UNION
Tritonia myrakeenae
stephens 89
Bathyliotina glassi
LOS ANGELES 1989
WESTERN SOCIETY OF MALACOLOGISTS

55TH ANNUAL MEETING
THE AMERICAN MALACOLOGICAL UNION
LOS ANGELES, CALIFORNIA
JUNE 25 - 30, 1989

The 55th annual meeting of the American Malacological Union will be a combined meeting with the Western Society of Malacologists, held June 25-30, 1989, in Los Angeles, California, at the Davidson Conference Center of the University of Southern California. Facilities at the Los Angeles County Museum of Natural History will also be used for some of the events. There are to be three choices for housing, the University Hilton, the Vagabond Motel, and the University dormitories, all very close to the Davidson Conference Center. In addition to the proximity of beaches and mountains, the Los Angeles area has a delightful summer climate in late June, almost never too hot or humid.

Three symposia are planned:

BIOLOGY OF PELAGIC GASTROPODS
(Organized by Dr. Roger Seapy)

SYSTEMATICS AND EVOLUTION OF WESTERN NORTH AMERICAN LAND MOLLUSKS
(Organized by Drs. F. G. Hochberg and Barry Roth)

BIOLOGY OF SCAPHOPODS
(Organized by Dr. Ronald L. Shimek)

In addition to the symposia, contributed papers, and poster presentations, scheduled events will include field trips, an outdoor barbecue, and a banquet.

For further information please contact:
James H. McLean
President, AMU
Los Angeles County Museum of Natural History
900 Exposition Boulevard
Los Angeles, California 90007, U.S.A.

(213) 744-3377

In Errata: Volume 6, No. 2, page 219: Under dates of publication and key, change "Volume 6, No. 2: July 1988 [6(2)]" to read "Volume 6, No. 2: October 1988 [6(2)]."

SPECIAL PUBLICATIONS OF THE *AMERICAN MALACOLOGICAL BULLETIN*

The Special Publication Series of the *American Malacological Bulletin* was begun to disseminate collected sets of papers with similar or related themes in a single volume. To date, three such issues have been published, each the result of a special convened symposium. The three Special Editions are *PERSPECTIVES IN MALACOLOGY, PROCEEDINGS OF THE SECOND INTERNATIONAL CORBICULA SYMPOSIUM,* and *PROCEEDINGS OF THE SYMPOSIUM ON ENTRAINMENT OF LARVAL OYSTERS.* Additional Special Editions are planned for the near future.

PERSPECTIVES IN MALACOLOGY (Sp. Ed. #1, July, 1985) offers a wide range of papers dealing with molluscan biology of interest to professionals and amateurs alike. These papers were presented as part of a symposium held in honor of Professor M. R. Carriker at the time of his retirement and highlight a variety of recent advances in numerous facets of the study of molluscs. *PERSPECTIVES IN MALACOLOGY* offers insight into some of the frontiers of molluscan biology ranging from deep-sea hydrothermal vent malacofauna to chemical ecology of oyster drills.

The *PROCEEDINGS OF THE SECOND INTERNATIONAL CORBICULA SYMPOSIUM* (Sp. Ed. #2, June 1986) contains numerous papers on this exotic bivalve that has become a significant ''pest'' organism of several power plants and other industries using cooling waters. The proliferation, spread, functional biology, attempts at industrial control, taxonomy, and many other topics of interest to the malacologist and industrial biologist are addressed in this important special publication.

The third special edition of the *American Malacological Bulletin, PROCEEDINGS OF THE SYMPOSIUM ON THE ENTRAINMENT OF LARVAL OYSTERS* (Sp. Ed. #3, October 1986) contains important review papers on the larval biology of the American oyster *Crassostrea virginica*, as well as intriguing papers on factors that limit productivity of these bivalves and limitations that exist on their dispersal and survival. The impact of cutter-head dredges is addressed in this special edition with special emphasis on the Chesapeake Bay system.

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GENETIC VARIATION IN *NEOTRICULA APERTA*, THE INTERMEDIATE SNAIL HOST OF *SCHISTOSOMA MEKONGI*: ALLOZYME DIFFERENCES REVEAL A GROUP OF SIBLING SPECIES

KATHARINE C. STAUB
DAVID S. WOODRUFF
DEPARTMENT OF BIOLOGY (C-016) AND
CENTER FOR MOLECULAR GENETICS
UNIVERSITY OF CALIFORNIA, SAN DIEGO
LA JOLLA, CALIFORNIA 92093, U.S.A.

E. SUCHART UPATHAM
VITHOON VIYANANT
CENTER FOR APPLIED MALACOLOGY AND ENTOMOLOGY
DEPARTMENT OF BIOLOGY, FACULTY OF SCIENCE
MAHIDOL UNIVERSITY
RAMA VI ROAD, BANGKOK 10400, THAILAND

ABSTRACT

Neotricula aperta (Temcharoen) is a highly variable pomatiopsid gastropod found in the Mekong River and its tributaries in Thailand. Three races and two other variant phenotypes have been described, originally as *Tricula aperta*. Samples of the sympatric alpha and gamma races from the Mekong River and of the beta race from the Mun River were characterized at 16 allozyme loci. Highly significant heterozygote deficiencies and differences in allele frequencies between males and females were apparent at many polymorphic loci in each of the three samples. The observed heterozygote deficiencies and sexual differences were artifacts produced by the presence of cryptic taxa in each original racial sample. In the Mun River beta race sample, we found two sibling species separated by a significant multilocus genetic distance (D = 0.22). In the Mekong River, the snails representing the alpha and gamma races were found to be referable to two other well differentiated sibling species (D = 0.34), both of which have individuals of "alpha" and "gamma" morphotypes. The Mekong River species pair are very well differentiated from the Mun River species pair (D = 0.74). Formal taxonomic revision of the *N. aperta* sibling species complex is postponed until topotypic material (*N. aperta* gamma race) from Laos can be examined. As only the "gamma race" had been shown to transmit *Schistosoma mekongi* naturally, it remains to be established which of the newly recognized species are epidemiologically significant.

The major Late Tertiary radiation of Triculinae (Prosobranchia: Rissoacea: Pomatiopsidae) in Southern China and Southeast Asia has resulted in more than 12 genera and 120 species of small freshwater snails (Davis, 1979, pers. comm., 1986; Kang, 1983, 1984a, b, 1986; Liu *et al.*, 1983). *Neotricula aperta* (Temcharoen) is the best known member of this extraordinary radiation as it is the intermediate host for the human blood fluke, *Schistosoma mekongi* Voge, Bruckner and Bruce. In this paper we will present evidence, based on multilocus allozyme variation, suggesting that *N. aperta* actually comprises a group of at least four sibling species.

The species was first described as *Lithoglyphopsis aperta* by Temcharoen (1971) and subsequently placed in the genus *Tricula* by Davis (1979), and *Neotricula* by Davis *et al.* (1986). These are small (2-4 mm shell length), dioecious, aquatic prosobranch snails. In their monograph, Davis *et al.* (1976) described three races of this species in Thailand and Laos on the basis of shell size, shape, and microsculpture, mantle pigmentation, developmental rates, radular traits,

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features of male reproductive anatomy, habitat and distribution. Kitikoon *et al.* (1981) described the last two traits of the three races in more detail. The alpha and gamma races are found, frequently together, along 300 km of the Mekong River. The beta race is found only in the Mun River (alternatively transliterated as Mool), a tributary of the Mekong in northeast Thailand. Shell size, shell shape, and mantle pigmentation have been the diagnostic characters used in field identification for the sympatric alpha and gamma races. Gamma race snails typically have four large, distinctive pigment spots on their mantles that are absent in alpha and beta race snails. Gamma race snails are also often smaller than sympatric alpha race snails; beta race snails are intermediate in size. In the Mekong River, alpha and gamma race snails occupy the same range of benthic microhabitats: from near shore to river center and also in seasonal pools on exposed rock islands. Beta race snails occur in and near rapids in the Mun River. Snails of all races are found on solid substrata (rocks and sticks) and never on sand, mud or algal strands.

Davis *et al.* (1976) discussed the possibility that the three races could be reproductively isolated from one another. They suggested that the beta race, with its allopatric distribution and pronounced microhabitat preferences, could be specifically distinct from the Mekong River races. They further speculated that differential rates of growth and maturation could act to isolate the sympatric alpha and gamma races reproductively, and that these two taxa also could have reached full species rank. They concluded, however, that their evidence for significant intraracial variation and for racial intermediacy did not support such conclusions. They argued that the known differences in the reproductive organs, shell size and sculpture, pigmentation, and radular formulae could simply reflect differences in ontogeny and ecology rather than genetically-based evolutionary divergence. They found apparent hybrids (snails with irregular pigment patterns and shell size and shape intermediate between the alpha and gamma races) at one locality and noted that the alleged anatomical differences between these races were somewhat artificial. Similarly, microhabitat preferences overlap broadly (Kitikoon *et al.*, 1981). Thus, no formal subspecific nomenclature was proposed to partition the variation recognized in this species from the outset.

This view of *Neotricula aperta* as a highly variable species with recognizable ecophenotypic races was subsequently challenged by Kitikoon's reports (1981a, b, 1982a, b; Kitikoon *et al.*, 1981) on additional phenotypic variation, chromosome numbers and karyotypes, isoenzyme patterns, and parasite compatibility. Kitikoon (1982b:55) suggested that 'the so-called alpha, beta, and gamma "races" of *T. aperta* are at least different subspecies and may well be different species.' Our quantitative population study of allozyme variation in this taxon supports the latter conclusion, but in a manner completely unanticipated in our preliminary report (Woodruff *et al.*, 1986b).

MATERIALS AND METHODS

Using distributional, ecological, and morphological criteria to identify snails in the field, samples of *Neotricula aperta* alpha, beta, and gamma races were collected in northeastern Thailand in May 1984. *N. aperta* alpha race and gamma race snails were taken from the Mekong River near Ban Bungkhong in the Khemarat District of Ubon Ratchathani Province. Alpha snails were found in pools on a rock island and gamma race snails were taken nearby from rocks cropping out in the main river channel where the water was deeper and the current swifter. In both cases, however, water depths in May were less than 1.0 m. *N. aperta* beta race snails were collected in the Mun River near Khaeng Khao in the Phibun Mangsuhan District of Ubon Ratchathani Province. This site is midway between the town of Ubon and the Mun's juncture with the Mekong and about 100 km directly south of the alpha-gamma collection site. Snails were taken from rocks in fast flowing water less than one meter deep. In every case, sampling was conducted along less than 10 m of river bottom. Racial identities were confirmed and snails were sexed under a binocular microscope in Bangkok soon after collection. Snails were then frozen at -70°C until electrophoresis was carried out at the University of California, San Diego in 1985. Voucher specimens were deposited in the museum at the Center for Applied Malacology, Mahidol University.

The electrophoretic techniques used are described in general terms elsewhere (Mulvey and Vrijenhoek, 1981; Woodruff *et al.*, 1988). Individual snails were quickly homogenized in less than 0.1 ml (2-3 drops from a standard Pasteur pipette) of grinding solution (0.01 M Tris, 0.001 M EDTA, 0.05 mM NADP, pH 7.0) with a glass rod. The homogenate was centrifuged at 10,000 g for 2 min in a Fisher 235A microcentrifuge, and the supernatant was absorbed onto 3 x 9 mm tabs of Whatman No. 3 chromatography paper which were then inserted into cold 12% Sigma® starch gels (one tab per snail per gel). Electrophoresis was carried out using four different buffer systems at 4°C for 15-18 hrs (Table 1). A bromophenol blue marker dye migrated 100-125 mm anodally during this time except in the case of buffer system Tris-Citrate pH 6.8 in which the marker migrated 70-100 mm. Following electrophoresis, 4-5 slices were cut from each gel and each slice was stained for a specific enzyme following standard methods (Shaw and Prasad, 1970; Harris and Hopkinson, 1978). The esterase substrate was alpha-napthyl acetate; the peptidase substrate was leucyl-alanine.

Electrophoretic conditions for the resolution of 12 enzymes coding for the 16 allozyme loci reported here are described in Table 1. These enzymes were selected on the basis of their interpretable electromorphs from about 30 enzymes tested under ten different electrolyte and pH conditions and are associated with a variety of metabolic pathways. Snails from different samples were run on each gel to facilitate commparisons; isozymes were numbered and allozymes assigned mobility values relative to the common electromorph in *Neotricula aperta* alpha race. In Table 6, alleles are listed in order of their decreasing anodal mobilities; cathodal mobility is indicated by a negative value. For each locus, relative mobilities are those for the first buffer system reported in Table 1. These are reported to two decimal places only where

Table 1. Electrophoretic buffers used for resolution of proteins in *Neotricula aperta*.

Enzyme (E. C. #)	Abbreviation	Buffer*
Acid phosphatase (3.1.3.2)	ACP	TC 6.8
Aspartate aminotransferase (2.6.1.1.)	AAT	TBE 8.0
Esterase (3.1.1.1)	EST-1	TBE 8.0
	EST-2	TBE 8.0
	EST-3	TBE 8.0
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GAP	AP 6.0, TC 6.8
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	GPDH	AP 6.0, TC 6.8
Glucose phosphate isomerase (5.3.1.9)	GPI	TC 6.0, TC 6.8
Isocitrate dehydrogenase (1.1.1.42)	IDH	TC 6.8
Leucine aminopeptidase (3.4.11)	LAP (PEP-2)	TC 6.0, TBE 8.0
Malate dehydrogenase (1.1.1.37)	MDH	TC 6.0
Peptidase (3.4.-)	PEP-3	TBE 8.0
	PEP-4	TBE 8.0
6-Phosphogluconate dehydrogenase (1.1.1.44)	PGD	AP 6.0
Phosphoglucomutase (5.4.2.2)	PGM-1	TC 6.0
	PGM-2	AP 6.0

*AP 6.0: 0.04 M citrate adjusted with N-(3-aminopropyl)-morpholine to pH 6.0; diluted 1:19 for gels and undiluted for electrodes (16 hr., 80 v). TBE 8.0: 0.5 M Tris, 0.65 M borate, 0.02 M EDTA, adjusted to pH 8.0; diluted 1:9 for gels and undiluted for electrodes (16 hr., 100 v). TC 6.0: 0.378 M Tris, 0.165 M citrate, adjusted to pH 6.0; 13.5 ml diluted to 400 ml for gel and undiluted for electrodes (16 hr., 60 v). TC 6.8: 0.188 M Tris, 0.065 M citrate, adjusted to pH 6.8: diluted 1:9 for gels and 1:5 for electrodes (16 hr., 150 v).

they cannot be distinguished by a single decimal place approximation. Commonly used enzyme abbreviations are typeset in capital letters to indicate the protein and in italics to indicate the presumed locus.

The mean number of alleles per locus (*A*), the proportions of loci polymorphic (a locus was considered polymorphic if more than one allele was detected,) *P*, and the mean individual heterozygosity (by direct count) (*H*), were calculated for each sample. Allozyme frequencies for the polymorphic loci were tested for their agreement with Hardy-Weinberg expectations for a panmictic population by X^2- test where appropriate and by the Fisher exact test. Allozyme frequency differences between sexes were also tested for significance by X^2- and *G*-tests. Genetic distance coefficients (*D*) (Nei, 1978; standard error after Nei *et al.*, 1985) and genetic similarity coefficients (*S*) (Rogers, 1972) were calculated and clustered by the UPGMA algorithm. X^2- and *G*-tests were performed with software accompanying Sokal and Rohlf (1981); other analyses were performed with the BIOSYS-1 computer program (Swofford and Selander, 1981).

The above analyses were first performed on the original "racial" samples with sexes pooled and then with sexes separated. As the original samples were found to be highly heterogeneous, it became necessary to repeat the analyses with the snails from each sample site resorted according to individual genotype. The sorting procedure, based on three or more diagnostic loci, is described below.

RESULTS

VARIATION IN THE THREE ORIGINAL SAMPLES SORTED INTO ALPHA, BETA AND GAMMA RACES

For reasons that will become clear below, the allele frequencies at all 16 presumptive loci are not reported here. These data on variation in the original alpha, gamma and beta "racial" samples are presented elsewhere (Staub, 1988).

Our preliminary analyses showed *Neotricula aperta* alpha race and gamma race samples were virtually indistinguishable at all loci ($D = 0.01 \pm 0.02$). In contrast, the mean genetic distance value between beta race and the two Mekong River races was unexpectedly large ($D = 0.66 \pm 0.24$). However, panmixia is an important assumption of Nei's genetic distance statistics and significant departures from Hardy-Weinberg expectations for panmixia were detected in 62% on the polymorphic loci in these samples (Table 2). In all 18 cases, there was a deficiency of heterozygotes and all but two tests were significant at the 1% ($p < 0.01$) level.

The ratio of females to males in the original racial samples was 32:36 for alpha race, 34:43 for beta race, and 32:34 for gamma race. In each original sample, the pattern of loci with heterozygote deficiencies was essentially the same within each sex as it was with the sexes pooled. Neither males

Table 2. Number of loci showing a significant deficiency of heterozygotes, as a fraction of the total number of polymorphic loci, before and after resorting *Neotricula aperta* racial samples by three-locus genotype.**

Original Samples		Resorted Samples	
alpha race	6(6)*/10	Mekong River taxon 1	2(0)/8
gamma race	7(6)/11	Mekong River taxon 2	2(2)/10
beta race	5(4)/8	Mun River taxon 1	0(0)/6
		Mun River taxon 2	4(2)/6

*Number of Fisher exact tests significant at $0.01 < p < 0.05$ and at $p < 0.01$ (in parentheses).

**See text and Tables 4 and 5 for full explanation.

nor females contributed more to any sample's overall deficiencies and no single-locus genotype appeared to be sex-linked for any sample. However, allele frequencies were notably different between the sexes at many loci. This too was unexpected as males and females allegedly represent a random sample of each population and sex-linked allozymes are rare (Richardson *et al.*, 1986). Tests of sample independence between male and female subsets revealed significant ($p < 0.05$) differences in each original sample (Table 3).

Although the initial analysis suggested that the *Gap*$^{1.0}$ and *Gap*$^{1.4}$ alleles were equally abundant in the alpha and gamma races (Staub, 1988), no heterozygotes were observed among 118 animals. Likewise, no *Pep-3*$^{1.2/1.0}$ heterozygotes were observed among 120 animals. Concordance by specific genotype between these two loci and a third with a marked deficiency of heterozygotes, *Gpi* (N = 126) was 100% (Table 4). Similarly, no heterozygotes were observed at three polymorphic loci in the beta race sample: *Lap* (N = 59), *Mdh* (N = 65), and *Pep-3* (N = 48) and the concordance by genotype between these three loci is also nearly complete (Table 5).

The unexpected differences between sexes and these striking associations among alleles at loci with no heterzygotes suggested that the original sample sorting had been insensitive to the genetic heterogeneity present at each locality. The snails from each original collecting locality were accordingly resorted by three-locus genotype, as identified in Tables 4 and 5, and the analyses were repeated. The original racial designations were abandoned.

Table 3. Number of loci showing a significant difference in allele frequencies between males and females, as a fraction of the total number of polymorphic loci, before and after resorting *Neotricula aperta* "racial" samples by three-locus genotype.**

Original Samples		Resorted Samples	
alpha race	6(2)*/10	Mekong River taxon 1	1(0)/8
gamma race	5(4)/11	Mekong River taxon 2	1(0)/10
beta race	2(1)/8	Mun River taxon 1	***
		Mun River taxon 2	2(0)/6

*Number of Fisher exact tests significant at $0.01 < p < 0.05$ and at $p < 0.01$ (in parentheses).

**See text and Tables 4 and 5 for full explanation.

***Sample size too small to analyze.

VARIATION IN MEKONG RIVER AND MUN RIVER SAMPLES FOLLOWING REASSORTMENT BY INDIVIDUAL MULTILOCUS GENOTYPE

The alpha race and gamma race samples were pooled as a Mekong River sample within which we discovered two genetically defined groups of individuals, hereafter called Mekong River taxon 1 and Mekong River taxon 2. Each of these newly recognized taxa includes snails previously referred to both alpha and gamma races. The ratio of alpha race to gamma race snails was 30:34 and 38:32 for taxon 1 and taxon 2 respectively; the ratio of female to male snails in the new taxa was 32:32 and 32:38, respectively.

Similarly, the snails in the Mun River sample originally referred to the beta race are hereafter assigned to two genetically defined groups: Mun River taxon 1 and Mun River taxon 2. The ratio of female to male snails was 3:8 and 31:31 for taxon 1 and taxon 2, respectively. Three snails had apparently intermediate genotypes but were assigned to taxon 2 on the basis of variation at *Mdh* and *Pep-3* only because the *Lap*$^{1.05}$ and *Lap*$^{1.0}$ electromorphs are too similar for reliable discrimination of all individuals. Four snails could not be assigned because they did not show activity for any of the three diagnostic enzymes.

Allele frequencies for the newly recognized taxa are displayed in Table 6 along with summary genetic variability statistics. The number of polymorphic loci is eight in Mekong River taxon 1 and ten in Mekong River taxon 2. There are striking differences in allele frequencies between these two taxa at *Est-1, Pep-4, Pgm-1,* and *Pgm-1*, as well as at the three loci (*Lap, Mdh,* and *Pep-3*) on which the reassortment was based -- in other words, at virtually all the polymorphic loci. This observation is quantified by the significant genetic distance value for the two taxa, D=0.34 ± 0.16.

Table 4. Genotypes at three electrophoretic loci for 134 snails originally referred to *Neotricula aperta* alpha race and *Neotricula aperta* gamma race, showing Mekong River taxon to which snails of each genotype were assigned.

	Locus			No. snails*		
Mekong River taxon	(118)** *Gap*	(126) *Gpi*	(120) *Pep-3*	N_3	N_2	N_1
1	1.4/1.4	1.0/1.0	1.2/1.2	42	10	2
1	1.4/1.4	1.0/1.0	1.2/1.11	4	3	0
1	1.4/1.4	1.0/1.0	1.11/1.11	3	0	0
2	1.0/1.0	2.0/2.0	1.0 /1.0	27	16	0
2	1.0/1.0	2.0/2.0	1.11/1.0	2	2	0
2	1.0/1.0	2.0/1.0	1.0/1.0	18	3	0
2	1.0/1.0	1.0/1.0	1.11/1.0	1	0	0
2	1.0/1.0	1.0/1.0	1.0/1.0	1	0	0

*N_3 = number of individuals scored at all three loci; N_2 = number scored at two of the three loci; N_1 = number scored at one locus.

**Total number of individuals scored at this locus shown in parentheses.

Among the Mun River taxa, formerly lumped as beta race, the number of polymorphic loci is five in Mun River taxon 1 and six in Mun River taxon 2 (Table 6). There are notable differences in allele frequencies between these two taxa at *Pgd* and *Est-3* in addition to the three loci (*Lap, Mdh,* and *Pep-3*) used to resort the original sample -- again, at virtually all the polymorphic loci. The genetic distance value for the two Mun River taxa is $D = 0.22$ * 0.12.

The newly recognized Mekong River taxa show markedly fewer heterozygote deficiencies than the original alpha race and gamma race samples (Table 2). There are residual deficiencies ($p < 0.05$) at *Lap* and *Pep-3* in Mekong River taxon 1 and at *Acp* and *Pep-4* in Mekong River taxon 2; two of these four positive tests are significant at the 1% level, those for *Acp* and *Pep-4* in Mekong River taxon 2. In the Mun River taxa, the number of loci showing a deficiency of heterozygotes is also reduced compared to the original beta race sample (Table 2). The sample of Mun River taxon 1 is too small to analyze. Deficiencies remain at *Est-1, Lap, Pgd,* and *Pgm-1* in Mun River taxon 2; two of the four positive tests are significant at the 1% level, those for *Est-1* and *Lap*.

Differences in allele frequencies between the sexes were eliminated by the reassortment of alpha and gamma races into Mekong River taxon 1 and 2 (Table 3). A difference ($0.01 < p < 0.05$) remains at the *Acp* locus for both Mekong River taxa. The effect of the beta race reassortment on sex differences in allele frequencies cannot be established for Mun River taxon 1 as the sample is too small to analyze ($N = 11$). In Mun River taxon 2, two loci (*Acp* and *Pgd*) show minor (and statistically insignificant) sex-related differences. In each of the four newly recognized taxa, the pattern of loci with heterozygote deficiencies is essentially the same within each sex as it had been for the sexes pooled. Neither males nor females contributed more to any sample's overall deficiencies and no single-locus genotype appeared to be sex-linked for any sample.

The genetic distance value between the Mekong River taxa and the Mun River taxa is very significant ($D=074 \pm 0.26$), as depicted in the phenogram (Fig. 1). Table 7 displays genetic distance and identity values for each of the six pairwise comparisons for the four taxa.

DISCUSSION

HETEROZYGOTE DEFICIENCIES AND THEIR INTERPRETATION

The validity of our conclusion depends on our interpretation of the massive heterozygote deficiencies as evidence for a type of sampling error commonly referred to as the Wahlund effect. However, a discussion of other reasons for heterozygote deficiencies is appropriate here as there are several other possibilities that demand critical consideration. Heterozygote deficiencies across most or all polymorphic enzyme loci have been reported for other mollusc populations, particularly among marine species (Johnson and Black, 1984; McMeekin, 1985; Singh and Green, 1984; Woodruff *et al.*, 1986a; Zouros and Foltz, 1984) and a number of potential causes have been considered. These can be roughly classified into two groups: first, true deficiencies of heterozygotes in natural populations and, second, apparent deficiencies due to sampling error or other experimental error. A true heterozygote deficiency at an enzyme locus could be due to (1) location of the locus on a sex chromosome (Zouros *et al.*, 1980), (2) complete or partial inbreeding (Hedrick and Cockerham, 1986), or (3) selection against heterozygotes, for instance, at a particular developmental stage (Singh and Green, 1984). There are, in addition, a number of ways in which heterozygote deficiency at a locus could be apparent, but not real, due to (4) scoring bias for homozygotes (Ayala *et al.*, 1973), (5) presence of one or more null alleles (Zouros *et al.*, 1980), (6) biased sampling of homozygotes, or (7) the so-called Wahlund effect (Singh and Green, 1984). Biased sampling of homozygotes could be due to (6a) genetic patchiness across a population's habitat at the time of collection, referred to as population subdivision by Zouros *et al.* (1980), or (6b) differential survival of homozygotes following collection. The Wahlund effect is the result of mixing representatives of two (or more) independent gene pools with differing allele frequencies in the same sample. It could be due to (7a) the existence of cryptic (sibling) taxa or (7b) error in field identification and taxonomic separation among already recognized taxa showing similar features. We consider each of these hypotheses in turn.

1. Real heterozygote deficiencies due to chromosomal constraints. The mechanism of chromosomal determination of sex in *Neotricula aperta* is not known but was speculated by Kitikoon (1982a) to be an XO-male/XX-female mechanism, based on chromosome pairing data. Such a system would result in an absence of heterozygotes in males at any X-linked locus. We did not find sex-linkage at any locus, either before or after the reassortment (29 and 24 tests, respectively). Moreover, such a system (or any other) does not predict the generalized (multilocus) strong genotypic disequilibria shown by our data.

2. Real heterozygote deficiencies due to inbreeding. Although self-fertilization is not possible in dioecious triculines, it is possible that partial inbreeding could be contributing to increased homozygosity in these snails. *Neotricula aperta* snails have low vagility and are substrate limited (Davis *et al.*, 1976); they are found packed tightly on solid substrata, often rocks, presumably where the eggs from which they hatched were deposited, and it is possible that sib matings occur with high frequency. The snails fit the profile of *r*-selected colonists whose patchily distributed habitats are changed annually when the monsoon flood raises river levels dramatically (up to 15 m in the Mekong) (Davis *et al.*, 1976). Female survivorship from the preflooding time of copulation to the postflooding time of egg deposition is low and founder effects could further increase the likelihood of sib matings. As inbreeding affects all loci in a uniform way, the generalized disequilibria shown by our data are consistent with this hypothesis. However, the complete absence of intermediates between the two genetically-defined Mekong River taxa negates this hypothesis.

3. Real heterozygote deficiencies due to natural selection.

Table 5. Genotypes at three electrophoretic loci for 74 snails originally referred to *Neotricula aperta* beta race, showing Mun River taxon to which snails of each genotype were assigned.

Mun River taxon	Locus			No. snails*		
	(59)** *Lap*	(66) *Mdh*	(46) *Pep-3*	N_3	N_2	N_1
1	1.0/1.0	0.5/0.5	1.2/1.2	5	6	0
2	1.05/1.05	1.0/1.0	1.09/1.09	26	24	9
2	1.0/1.0†	1.0/1.0	1.09/1.09	3	0	0

*N_x - number of individuals scored at all three loci; at two of the three loci; at one locus.

**Total number of individuals scored at this locus shown in parentheses.

†See text for explanation.

Constructing reasonable selection hypotheses is difficult because we lack adequate quantitative data on the ecology and behavior of *Neotricula aperta*. These snails have a life span of approximately one year, and one might expect strong selection for competitive ability during the two month period of explosive population growth and high juvenile mortality. Differences in growth rates have, in fact, been noted between "races" and sexes (Davis *et al.*, 1976) and between localities (Kitikoon *et al.*, 1981). Relationships between heterozygosity and growth have been suggested for many other organisms including several marine molluscs (see review by Allendorf and Leary, 1986). Testing this hypothesis, like the previous one, would require continuous ecobehavioral and demographic observations in nature and samplng that is very sensitive to local population structure.

4. Artificial heterozygote deficiencies due to gel scoring errors. We are highly confident of our scoring for the enzymes on which the reassortment of the original "racial" samples was based: GAP, PGI, and PEP-3 in the alpha race and gamma race samples and MDH and PEP-3 in the beta race sample all form clear, distinct bands. On the other hand, some of the residual heterozygote deficiencies could be explained by scoring bias for homozygotes: ACP and PEP-4 in Mekong River taxon 2 and EST-1 and LAP in Mun River taxon 2. ACP electromorphs were diffuse and never clearly double-banded. In the case of PEP-4, there were only slight mobility differences between five electromorphs, making presumptive heterozygotes difficult to discern and, therefore, possibly underestimated. EST-1 banded faintly and diffusely, never being clearly double-banded. The two LAP electromorphs seen in the Mun River taxa were very close in mobility and it is possible that heterozygotes were not recognized. Even with these minor qualifications scoring bias cannot account for our observations.

5. Artificial heterozygote deficiencies due to null alleles. There was no evidence for a common null allele at any locus in any of the original "racial" samples: The missing data for unscorable snails (Tables 4 and 5) did not assume the random pattern expected for non-lethal null allele homozygotes or codominant null allele heterozygotes but tended to occur together on inferior gels. If null homozygosity was lethal at a locus, this could account for a heterozygote deficiency even if blank spots, due to other causes, appear on gels. However, lethal or sublethal null alleles would have to originate by mutation at unrealistically high rates or have unreasonably high selection coefficients to explain the levels of heterozygote deficiency shown by the loci in our study. It seems highly unlikely that null alleles, lethal or not, could account for the generalized strong genotypic disequilibria shown by our data.

6a. Artificial heterozygote deficiencies due to biased sampling of homozygotes. The possibility that one or more of the original "racial" populations was genetically subdivided in some ecobehavioral way at the time of collection was entertained. If, for instance, a snail's selection of microhabitat is correlated with its growth and growth rate is in turn associated with heterozygosity at one or more loci then it could be possible to simply miss a highly heterozygous portion of the population if the sampling protocol is not carefully designed. However, the general hypothesis (Zouros *et al.*, 1980) does not require the degree of genetic differentiation seen in our data, and for this reason alone we think it unlikely to account for the pervasive heterozygote deficiencies seen in all three of our original samples. Again, the very high genetic identity (D = 0.01) between the original "alpha race" and "gamma race" samples and the complete lack of intermediacy between the two Mekong River taxa as we have defined them (Table 4) argues against this less-than-dramatic sort of population structuring.

6b. Artificial heterozygote deficiencies due to differential survival of genotypes following collection. Our snails were maintained in aquaria according to established culture methods (Kitikoon, 1981a) for about one month following collection and then frozen. Artificial selection due to collecting, sorting, and live maintenance procedures is always a concern in this type of study. Although we have no quantitative information on snail mortality during this one month period, it was not excessive and we doubt artificial selection accounts for our observations.

7a. Artificial heterozygote deficiencies due to the unsuspected presence of cryptic taxa in the allegedly homospecific samples. The sampling error known as the Wahlund effect (Wahlund, 1928) is the hypothesis we think best accounts for the heterozygote deficiencies in the original "racial" samples and is, of course, the premise on which our sampling reassortment was made. The complete lack of heterozygotes without concomitant evidence for null alleles or sex-linkage at not one but several loci strongly support this hypothesis. If the heterozygote deficiencies in the original samples were real, we would not expect such a marked reduction in the pattern

Table 6. Allele frequencies for 16 loci in four resorted samples of *Neotricula aperta*, with summary statistics of genetic variability.*

	Mekong River		Mun River	
locus/allele	Taxon 1	Taxon 2	Taxon 1	Taxon 2
Aat	(51)**	(55)	(2)	(14)
1.0	1.00	1.00		
0.9			1.00	1.00
Acp	(53)	(56)	(9)	(38)
1.1	0.40	0.24	0.11	0.14
1.0	0.42	0.65	0.78	0.75
0.7	0.18	0.11	0.11	0.11
Est-1	(52)	(60)	(9)	(53)
1.0	0.32	0.72		
0.93	0.68	0.28	0.17	0.07
0.88			0.78	0.85
0.81			0.05	0.08
Est-2	(43)	(59)	(8)	(51)
1.0	1.00	1.00	1.00	1.00
Est-3		(56)	(64)	(9)
1.6				0.01
1.4		0.02	0.94	0.99
1.0	1.00	0.98	0.06	
Gap†	(55)	(61)	(9)	(42)
1.4	1.00		1.00	1.00
1.0		1.00		
α-*Gpdh*	(28)	(52)	(6)	(10)
1.0	1.00	1.00	1.00	1.00
Gpi†	(63)	(61)	(11)	(55)
2.0		0.80		
1.0	1.00	0.20	1.00	1.00
Idh	(62)	(64)	(10)	(48)
1.0	1.00	1.00	1.00	1.00
Lap††	(61)	(61)	(11)	(48)
1.1	0.6			
1.05				0.92
1.0	0.93	0.97	1.00	0.08
0.8	0.01	0.03		
Mdh††	(61)	(66)	(10)	(56)
1.0	1.00	1.00		1.00
0.5			1.00	
Pep-3†/††	(57)	(62)	(6)	(40)
1.2	0.89		1.00	
1.11	0.11	0.04		
1.09				1.00
1.0		0.96		
Pep-4	(59)	(64)	(9)	(54)
1.14		0.08		
1.07	0.10	0.48		
1.0	0.26	0.29		
0.96			1.00	1.00
0.9	0.35	0.14		
0.8	0.29	0.01		
Pgd	(51)	(64)	(10)	(41)
1.8	0.47	0.04		
1.6			0.05	0.02
1.0	0.53	0.96	0.85	0.60
0.5			0.10	0.38
Pgm-1	(45)	(54)	(4)	(21)
1.07			0.87	0.95
1.0	0.97	0.15	0.13	0.05
0.9	0.03	0.85		

(continued)

Table 6. (Continued)

	Mekong River		Mun River	
locus/allele	Taxon 1	Taxon 2	Taxon 1	Taxon 2
Pgm-2	(50)	(55)	(11)	(31)
-0.7	0.20	0.17		
-0.9	0.34	0.10		
-1.0	0.46	0.46		
-1.1		0.27	1.00	1.00
N	52.9	59.9	8.4	40.2
(S.E.)	(2.2)	(1.1)	(0.7)	(3.6)
A	1.8	2.0	1.5	1.6
P	50.0	62.5	31.3	37.5
H	0.18	0.15	0.09	0.05

*Samples are described in text; *N* = mean sample size (and standard error) per locus, *A* = mean no. alleles per locus, *P* = proportion of loci polymorphic, *H* = mean individual heterozygosity.

**Sample size.

†One of the loci used to characterize the newly recognized Mekong River taxa.

††One of the loci used to characterize the newly recognized Mun River taxa.

following reassortment (Table 2). Instead, we would expect to see random changes among loci. The same sort of reasoning applies to the decrease in the number of loci showing significant differences in allele frequencies between males and females. The virtual absence of these sexual differences in our resorted samples (Table 2) argues that they and not the original racial samples best represent the natural taxa present.

7b. Artificial heterozygote deficiencies due to errors in field identification and the inclusion of several previously recognized taxa in allegedly homospecific samples. We discuss this hypothesis last as, if correct, it would seriously compromise our conclusions. Two species found in the Mekong River have been reported to be similar enough to *Neotricula aperta* in size, shell shape, and mantle pigmentation to confuse collectors (Temcharoen, 1971; Davis *et al.*, 1976). *"Manningiella" conica* is closely related to or congeneric with *Tricula* (sensu lato; Davis, 1979; Kitikoon, 1981b) but so far has only been found at Khong Island, southern Laos (Davis *et al.*, 1976; Kitikoon *et al.*, 1981; Kitikoon, 1984), some 200 river km south of the site where we collected our alpha and gamma race samples. Moreover, it is most often found by sieving sand, a substratum not associated with *N. aperta (Davis et al.*, 1976). It has also been suggested that *Pachydrobia bavayi* could also be confused with *N. aperta* since its young have a shell very similar to that of *"M" conica* (Davis *et al.*, 1976; Upatham *et al.*, 1983). We think that the possibility of a generic misidentification is remote as, in the Mekong River in May, *Pachydrobia* sp. are typically 2-3 times the size of *N. aperta* and associated with soft-bottom microhabitats (Davis, 1979).

We conclude that the observed heterozygote deficiencies were most probably artificial and due to the insensitivity of our field sampling, and field and laboratory sorting to detect the previously unrecognized cryptic taxa coexisting at each site. We accordingly proceed to discuss the significance of the observed genetic distances between these newly discovered taxa.

Table 7. Matrix of genetic similarity and distance coefficients for four newly recognized taxa previously referred to *Neotricula aperta**.

Sample	1	2	3	4
1 Mekong River taxon 1	---	0.67	0.56	0.51
2 Mekong River taxon 2	0.34	---	0.44	0.42
3 Mun River taxon 1	0.54	0.84	---	0.78
4 Mun River taxon 2	0.68	0.88	0.22	---

*Below diagonal: Nei's (1978) unbiased genetic distance (*D*); above diagonal: Roger's (1972) genetic similarity (*S*).

TAXONOMIC INTERPRETATION OF MULTILOCUS GENETIC DISTANCES

As shown in Figure 1, we have detected two well-differentiated (*D* = 0.34) sympatric taxa in the Mekong River. In the Mun River, we discovered two other well-differentiated (*D* = 0.22) sympatric taxa. The newly recognized taxa within each river are more closely related to one another than to the taxa in the other river (*D* = 0.74). These estimates of genetic differentiation are based on 16 loci and a technique appropriate to establishing evolutionary relationships among congeneric taxa (Richardson *et al.*, 1986; Nei, 1987).

At the outset it must be stressed that there is no simple relationship between a Nei's genetic distance (*D*) value and taxonomic level. Other factors including innate genetic variability, mating system, effective population size and degree of population subdivision will all affect the rate of genetic divergence in a clade. Nevertheless, much can be learned from the vast literature on genetic differentiation within and between other well-characterized amphimictic (sexually reproducing, outcrossing and moderately polymorphic) species. For example, Thorpe (1983) reviewed over 7000 comparisons of conspecific populations of plants and animals and found that only 2% of the intraspecific *D* values exceeded 0.10. In contrast, he found that the average interspecific genetic distance in 900 congeneric comparisons was about 0.40 (range: 0.03 - >1.0). A survey of 23 genera of amphimictic

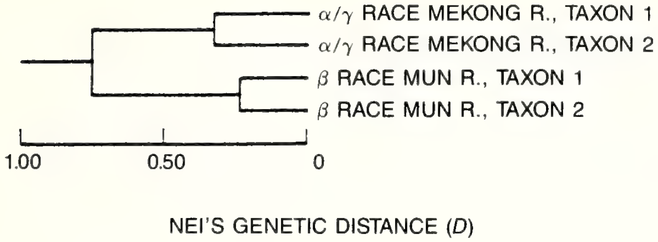
α/γ RACE MEKONG R., TAXON 1
α/γ RACE MEKONG R., TAXON 2
β RACE MUN R., TAXON 1
β RACE MUN R., TAXON 2
1.00
0.50
0
NEI'S GENETIC DISTANCE (D)

Fig. 1. Dendrogram showing relationship of four newly recognized sibling species previously referred to *Neotricula aperta*, generated by UPGMA cluster analysis based on 16 loci.

molluscs revealed they too typically have intraspecific genetic distances of <0.10 and congeneric interspecific genetic distances in the range 0.20 - 0.80 (Woodruff *et al.*, 1988). We conclude that our estimates of genetic differentiation within the taxon formerly called *Tricula aperta* are of such magnitude that each of the four newly discovered taxa warrant recognition as separate full species. Our only reservation about this recommendation arises from the lack of data on intraspecific variability within each of these sibling species. If, as expected, intraspecific variation is small ($D < 0.10$), and the gap between intraspecific and interspecific genetic distances remains relatively large, then the genetic distance values alone indicate these taxa are evolving separately as different biological species.

There is, of course, nothing new about the use of allozyme electrophoresis to detect sibling species. Bullini (1983) and Ayala (1983) review the successful use of the technique in the detection of sibling species in ascarid worms, plethodontid salamanders, *Anopheles* mosquitoes and *Drosophila*. Other examples involve the Asian schistosomes transmitted by snails of the genera *Tricula, Robertsiella* and *Oncomelania* (Fletcher *et al.*, 1980; Woodruff *et al.*, 1987a; Merenlender *et al.*, 1987). Studies of allozyme variation used in conjunction with traditional methods have been particularly useful in resolving the evolutionary relationships of taxonomically difficult groups of molluscs (Woodruff and Gould, 1980, 1987; Gould and Woodruff, 1986, 1987; Woodruff *et al.*, 1987b; Klinhom, 1989; Palmer, Gayron and Woodruff, unpub. data). Davis (1983, 1984) has used electrophoretic data to detect sibling species in other molluscs, but did not include this technique in his early studies of the triculines.

OTHER EVIDENCE THAT *NEOTRICULA APERTA* COULD BE A COMPOSITE TAXON

Kitikoon (1982a) described extraordinary variation in chromosome number and appearance for each on the so-called races of *Neotricula aperta*. Haploid chromosome numbers ranged from 13 to 17 in alpha race males, from 14 to 17 in beta and gamma race males, and from 16 to 17 in alpha and gamma race females. Diploid chromosome numbers were 29, 31, and 33 in alpha and gamma race males, 31 and 33 for beta race males, and 32 and 34 in alpha and gamma race females. Only beta race females showed no variation with 17 haploid and 34 diploid chromosomes. The pairing patterns at prophase I were also variable as were other aspects of the karyotype. This degree of variation within a single species is almost unknown (White, 1973) and suggests that Kitikoon's samples could have been as heterogeneous as our own. A new analysis based on allozymically sorted specimens could provide more coherent results.

Kitikoon's (1982b) electrophoretic study of 5 enzymes in the three races also revealed considerable interracial variation, but his results cannot be interpreted genetically as he pooled tissues of 40-100 snails to prepare his racial samples.

Kitikoon's work was based primarily on field collections made in 1972-4 and in 1979. In addition to recognizing the three so-called races, and noting the occurrence of some populations that did not conform to this classification, he distinguished two additional phenotypes of the gamma race from Sompamit Falls, southern Laos (Kitikoon and Schneider, 1976; Kitikoon *et al.*, 1981). He subsequently referred to the latter as (unnamed) separate species (Kitikoon, 1984). Clearly, both he and his colleagues recognized the complexity of the taxon called *Neotricula aperta*.

PARASITOLOGICAL IMPLICATIONS

So far only the gamma race has been unequivocally shown to transmit *Schistosoma mekongi* naturally (Kitikoon *et al.*, 1973), but the alpha and beta races are susceptible to miracidia infection with subsequent cercarial shedding in the laboratory (Kitikoon, 1981b; Yuan *et al.*, 1984). Several authors have compared rates of snail susceptibility but with inconsistent results (see Kitikoon, 1981b). However, there seems to be general agreement that, in the laboratory, beta race snails are highly susceptible, alpha race snails have low susceptibility, and gamma race snails are intermediate with respect to this trait (Kitikoon, 1981b). As host-parasite compatibility evolves on a very localized geographic basis in nature (Rollinson and Southgate, 1985; Woodruff, 1985), these laboratory experiments tell us rather little about the potential for the spread of human schistosomiasis from the transmission site at Khong Island, Laos. Our findings suggest that the identity of the intermediate host snail must now be reestablished and the epidemiological significance of its sibling species reinvestigated.

CONCLUSIONS

It is now apparent that there are two discrete taxa present in the Mekong River that do not coincide genetically with the so-called alpha and gamma races of *Neotricula aperta*. Similarly, in the Mun River we discovered two sibling species presently confused under the name of the beta race of *N. aperta*. The genetic distances between these four taxa are large enough for us to conclude that all have reached the rank of full species. The lack of evidence for intermediacy in diagnostic allozyme characters support this. Formal taxonomic revision must, however, await the confirmation of these patterns by more careful recollection in the field and reexamination of the anatomy, morphology and karyotypes of the genetically defined taxa. The type locality of *N. aperta* is

Khong Island, Laos, and the holotype conforms to the so-called alpha race (Davis *et al.,* 1976). Until snails from this area can be recollected, it is unlikely that we can resolve the issues raised by this study of genetic variation in Thai animals.

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CELLULAR DNA CONTENTS OF THE FRESHWATER SNAIL GENUS *SEMISULCOSPIRA* (MESOGASTROPODA: PLEUROCERIDAE) AND SOME CYTOTAXONOMICAL REMARKS

HIROSHI K. NAKAMURA[1]
DEPARTMENT OF ZOOLOGY, FACULTY OF SCIENCE
KYOTO UNIVERSITY, KYOTO 606, JAPAN

YOSHIO OJIMA[2]
DEPARTMENT OF BIOLOGY, KWANSEI GAKUIN UNIVERSITY
UEGAHARA, NISHINOMIYA 662, JAPAN

ABSTRACT

The cellular DNA contents from eight Japanese *Semisulcospira*: *S. libertina* (Gould) and *S. reiniana* (Brot) of the *S. libertina* group, a widely distributed species complex in the Japanese Islands; and *S. decipiens* (Westerland), *S. habei* Davis, *S. morii* Watanabe, *S. multigranosa* (Boettger), *S. niponica* (Smith) and *S. reticulata* Kajiyama and Habe of the *S. niponica* group, the Lake Biwa endemic species complex, were measured by microfluorometry with DAPI staining. Although the species of the *S. libertina* group (2n=36 and 40) and those of the *S. niponica* group (2n=14, 24, 26 and 28) had been reported to have very different chromosome number, the measured DNA values were nearly the same, 3.4 ~ 3.7 pg/diploid. Hence it is deduced that karyotypical evolution resulting in different chromosome numbers between two species groups and within each group could occur without large genomic alternation.

Freshwater prosobranch snails of the genus *Semisulcospira* are a diverse and conspicuous element of the freshwater fauna of the Far East Asia. In Japan they are most abundant in springs, spring-fed rivers and streams (Kuroda, 1929). The taxa are relegated to two species groups, the *S. libertina* group, including widely distributed species in the Japanese Islands, and the *S. niponica* group, including many endemic species of Lake Biwa (Davis, 1969).

There is a wide variation in chromosome numbers within the genus *Semisulcospira*. This is remarkable because constancy of chromosome numbers within large taxa has been pointed out frequently in various molluscan groups (Patterson, 1969; Nakamura, 1985). In the present study, we measured the cellular DNA contents of eight species of *Semisulcospira* and examined whether the difference of the chromosome number in the genus could reflect changes in the genome size. As chromosomal rearrangement and karyotypical alteration have been thought to be essential in *Semisulcospira* speciation (Boss, 1978), data presented here allow a first assessment of this condition with regard to cellular DNA contents and chromosomes.

MATERIALS AND METHODS

Specimens of *Semisulcospira* spp., except *S. libertina*, were collected from Lake Biwa in August, 1988 and identified by N. C. Watanabe. Table 1 shows the localities and dates of collection. Cells of the embryos in the pallial brood pouch of two females of each species were prepared and examined by DNA microfluorometry with DAPI (4', 6-diamidino-2-phenylindole) staining of Komaru *et al.* (1988) with slight modifications:

1) Crack off the individual adult shells, and entirely dissect out the pallial brood pouches.
2) Place the individual brood chamber in a separate vial filled with 0.25% trypsin prepared in calcium and magnesium free phosphate buffer solution (PBS) and crush the embryonic shells with a glass rod.
3) Allow the trypsin to act on the embryonic body tissue in the vial over a magnetic stirrer at room temperature for 30 min.
4) Decant the contents into a 15 ml centrifuge tube and spin

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[1] Present address and reprint requests: Takasago Research and Development Center, Mitsubishi Heavy Industries, Ltd., 2-1-1 Shinhama, Arai-Cho, Takasago 676, Japan.

[2] Present address: Japan Fish Bioscience Institute, 1-17 Iwakunicho, Ashiya 659, Japan.

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at 100xg for 7 min.

5) Discard supernatant and wash cells once in PBS.
6) Fix in freshly mixed Carnoy's fixative (3:1 methanol-glacial acetic acid) by slow addition for 5 min.
7) Centrifuge and change the fixative three times and finally resuspend pellet.
8) Add one drop of cell suspension to a clean washed glass slide and air dry.
9) Stain the cells left on the slide with the DAPI solution for 1 hr at 4°C.
10) Mount the stained slide with the DAPI solution, cover with a cover slide, and seal with clear manicure cement. DAPI solution contained 50ng/ml 4', 6-diamidino-2-phenylindole dihydrochloride and 10mM 2-mercaptoethylamine hydrochloride in Tris buffer (10mM Tris, 10mM EDTA-2Na, 100mM NaCl, pH 7.4).

Though the absolute cellular DNA concentration for more than 110 molluscan species was reported by Hinegardner (1974), few of them are available in Japan. Therefore, we used goldfish (*Carassius auratus* Temmick and Schlegel) cells as the standard to estimate absolute DNA amounts of our snails. The fin epithelium of *C. auratus* was fixed and prepared in the same way as mentioned above.

Cell nuclei stained with DAPI were excited by ultra violet light (365nm) with an Olympus fluorescence microscope BHS-RFX. The optical conditions were as follows: excitation filter UGI, dichroic mirror DM400, cut filter L420, objective lens UVFL 40x.

Table 1. Collection data of specimens studied here.

Semisulcospira libertina group*	
S. libertina (Gould, 1859)	Uegahara Waterway (western side of the Kwansei Gakuin University campus), Nishinomiya City, Hyogo Pref., 10 Mar 1988.
S. reiniana (Brot, 1876)	Lake Biwa, around Hydrobiological Station, Kyoto Univ., Otsu City, Shiga Pref., 5 Aug 1988.
S. niponica group*	
S. decipiens (Westerland, 1883)	Lake Biwa, from a stretch of the lake about 1 km off shore (from Shina to Shimo-sakamoto section), Shiga Pref., 5 Aug 1988.
S. habei Davis, 1969	Lake Biwa, Konohama Beach, Moriyama City, Shiga Pref., 5 Aug 1988.
S. morii Watanabe, 1984	Lake Biwa, Chikubu-jima Island, Shiga Pref., 3 Aug 1988.
S. multigranosa (Boettger, 1866)	Lake Biwa, mouth of Kusatsu River, Kusatsu City, Shiga Pref., 3 Aug 1988.
S. niponica (Smith, 1876)	Lake Biwa, Uchide-hama Beach, Otsu City, Shiga Pref., 2 Aug 1988.
S. reticulata Kajiyama and Habe, 1962	Lake Biwa, from a stretch of the lake about 1 km off shore (from Shimo-sakamoto to Shina section), Shiga Pref., 5 Aug 1988.

*According to Davis (1969).

RESULTS

We were able to obtain very consistent fluorescence intensity measurements, because the fluorescence from DAPI stained cells was very intense and mounting the slides with DAPI solution reduced its decay (Hamada and Fujita, 1983). The results of DNA estimates of the eight *Semisulcospira* species are shown in Table 2. The value relative to the goldfish standard was converted to an estimate of DNA/nucleus by multiplying the DNA value in the goldfish nucleus by 4.0 pg/diploid (Hinegardner, 1972). The estimated DNA quantities, 3.4 ~ 3.7 pg/diploid, were not as variable as the chromosome numbers among the species, 2n=14 ~ 40; and there was little interspecific variation.

DISCUSSION

The microfluorometric procedure with DAPI staining is simple and useful for quantification of DNA content. Recently, this method has been successfully applied to measure the ploidy of a variety of molluscs; pearl oyster larvae, *Pinctada fucata martensii* (Uchimura, *et al.*, 1987) and scallop, *Chlamys nobilis* (Komaru, *et al.*, 1988). It has been demonstrated to be convenient and sufficiently accurate to be a substitute for flow cytometry. Using this procedure, we have determined the nuclear DNA content of eight species of *Semisulcospira*. The snails were shown to possess 3.4 ~ 3.7 pg/diploid, which is within the limits of the DNA values reported previously for the Mollusca and more specifically the Mesogastropoda. These values are slightly higher but close to the upper limit (about 3.2 pg/diploid) of the distribution (Hinegardner, 1974).

Davis (1969) subdivided Japanese *Semisulcospira* into two species groups: the *S. libertina* group and the *S. niponica* group. The former includes widely distributed species in the Japanese Islands and is characterized by larger chromosome numbers (n=18 or 20), many basal cords and many embryos per female. The latter consists of several endemic species of Lake Biwa and is characterized by smaller chromosome numbers (n=7 to 14), fewer basal cords and fewer embryos per female. Japanese *Semisulcospira* show considerable variety in chromosome numbers (Burch, 1968) and have therefore attracted our attention, because a general conservativeness with regard to chromosomal change is evident in many molluscan groups (Patterson, 1969; Nakamura, 1985, 1986).

In the present investigation we have measured the cellular DNA amounts to ascertain if the genome can change among the species as their chromosome number changes. We have found that the DNA values were very constant; independent of the divergence in chromosome numbers. Hence we infer that the difference in chromosome number could occur without large genomic alteration between the two species groups and within each group.

Boss (1978) interpreted that the reduction in chromosome number could have occurred in the karyotype of the Lake Biwa endemic species as a consequence of Robertsonian type of chromosomal rearrangement. This

Table 2. Cellular DNA contents in *Semisulcospira* spp. and *Carassius auratus*.

Species	Number of cells examined from all indiv.	DNA value relative to the goldfish (mean ± S.E.)	Estimated DNA per cell (pg/diploid)	Diploid chromosome number*1(2n); arm number (NF)
S. libertina	216	89.0 ± 1.3	3.6	2n=36; NF=72 (66*2)
S. reiniana	198	91.3 ± 0.9	3.7	2n=20
S. decipiens	174	84.6 ± 0.9	3.4	2n=24; NF=44
S. habei	251	86.0 ± 1.2	3.4	2n=14; NF=28
S. morii	144	86.6 ± 1.0	3.5	2n=32; NF=60*3
S. multigranosa	233	89.9 ± 1.1	3.6	2n=28; NF=28
S. niponica	214	87.6 ± 1.0	3.5	2n=24; NF=44
S. reticulata	288	93.6 ± 1.1	3.7	2n=24; NF=24
C. auratus	305	100.0 ± 0.8	4.0*4	——

*1after Burch (1968), but NF's calculated by the present authors.
*2-calculated according to the karyotype reported by Kobayashi (1986).
*3-calculated according to the karyotype reported by Watanabe (1984).
*4-after Hinegardner (1972).

phenomenon has been observed in many insect groups (see White, 1978 for examples) and it is assumed that their DNA contents remained essentially constant.

Although the constancy of DNA content was confirmed in the present study, something more complex and involving chromosomal alterations, is probably taking place. This has also been pointed out by Boss (1978). In the case of Robertsonian processes, the arm numbers or so-called the NF's ("nombre fundamental" of Matthey, 1945) of the chromosomes should correspond to the different chromosome numbers for all species. At the least, there would be much closer correlation among NF's than the chromosome numbers. Table 2 shows that there seems to be no relationship between the chromosome number and the NF in this group. For situations like this, Matthey (1973) presents some other possible explanations, especially for lower chromosome numbers, e.g. tandem fusion of the several smaller chromosomes producing one larger chromosome. Much more detailed information on the karyotypes, however, is needed to determine if such phenomena were applicable to the karyotypical evolution in the *Semisulcospira*. The size of each chromosome complement and other characteristics, such as banding patterns, to identify homologous chromosomes among the different species are left for the future studies.

Recently, Kobayashi (1986) reported very different results on karyotypes than those of Burch (1968), including chromosome number. One of the Lake Biwa endemic species, *S. nakasekoae*, was presented to have not smaller, but slightly larger chromosome number, 2n=38, than *S. libertina*, a typical representative of the widely distributed species. However, as incorrect and inconsistent use of chromosome terminology was used in the text, figures and tables, the article is partially difficult to understand. Watanabe (1984) reported a new chromosome number, 2n=32, in the genus from a new Lake Biwa endemic species, *S. morii*; however, this result was misquoted by Kobayashi (1986). Although karyological condition remains very complicated, the present study leads us to assume that the genome size cannot be changed largely within the *Semisulcospira*. This could provide a basis for investigating the mechanisms of the diversification in this group, and to accumulate more chromosomal information together with reexamination on the species previously studied by Burch (1968).

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USE OF SHELL MORPHOMETRIC DATA TO AID CLASSIFICATION OF *PISIDIUM* (BIVALVIA: SPHAERIIDAE)

BRUCE W. KILGOUR
DENIS H. LYNN
GERALD L. MACKIE
DEPARTMENT OF ZOOLOGY, UNIVERSITY OF GUELPH,
GUELPH, ONTARIO, CANADA, N1G 2W1

ABSTRACT

Univariate and multivariate statistical techniques were applied to 13 shell measurements of clams from a total of nine populations of four species of *Pisidium*. Using morphometric data, *P. compressum* (Prime, 1852) and *P. subtruncatum* (Malm, 1855) can be separated from each other, and from *P. adamsi* (Stimpson, 1851) and *P. casertanum* (Poli, 1795). *P. adamsi* and *P. casertanum* can be separated using morphometric data if they are collected from the same location. However, classification of these two species is difficult when shells from different habitats are compared.

In the Sphaeriidae, there are few discontinuous variables that can be successfully used to discriminate among species. As such, identification in the past has been based on shell shape but using subjective criteria (Herrington, 1962; Clarke, 1973; Burch, 1975; Mackie *et al.*, 1980). Since there tends to be variation in the form of shells among populations (Holopainen and Kuiper, 1982; Bailey *et al.*, 1983; Mackie and Flippance, 1983), and differences between species can be subtle, there is potential for mis-identification of clams.

Pisidium casertanum (Poli, 1795) is considered by many authors as the most widespread and common of the Sphaeriidae. According to Herrington (1962), Burch (1975), and Holopainen and Kuiper (1982), this species, also, exhibits the greatest variation in shell form among populations. Accordingly, species that are morphometrically similar to *P. casertanum* can be difficult to identify correctly. One such species is *P. adamsi* (Stimpson, 1851). According to Mackie (1989), *P. adamsi* has a longer dorsal margin that is more gently curved and has a steeper anterior slope than *P. casertanum*. Using these characters, these two species are still difficult to separate. Therefore, it is necessary that more objective means be used for description of these two species.

Typically, length, height and width are used to objectively describe shell shape in bivalves (e. g. Eager, 1978; Eager *et al.*, 1984; Mackie, 1989). However, using ratios of these measurements, shapes of *Pisidium casertanum* and *P. adamsi* are not significantly different from each other (Mackie, 1989). It is necessary, therefore, to develop new measurements that will more accurately describe shell shape for sphaeriid bivalves.

Pisidium compressum (Prime, 1852) and *P. subtruncatum* (Malm, 1855) are species that are more easily identified using shell shape. In this study, 14 morphometric measurements of five populations of *P. casertanum*, two populations of *P. adamsi* and one each of *P. compressum,* and *P. subtruncatum* were collected to determine if shell morphometric data can be used to separate species of *Pisidium*.

METHODOLOGY

SPECIMEN COLLECTION

Pisidium adamsi, P. casertanum, P. compressum, and *P. subtruncatum* were collected from 0.1-1.0 m depths of water with hand sieves (maximum opening 0.7 mm) from six locations in Ontario, during May, 1987: Aberfoyle Creek (43°28'N, 80°09'W); Carp River (45°29'N, 76°14'W); Golden Lake (45°34'N, 77°21'W); Hanlon Pond (43°33'N, 80°15'W); White Lake (45°34'N, 77°21'W); and Yantha Lake (45°30'N, 77°37'W) (Table 1). Shell form in the Sphaeriidae is affected by water hardness (Mackie and Flippance, 1983) and habitat type (Bailey *et al.*, 1983). Therefore, *P. casertanum* were collected from habitats exhibiting a range of hardness and habitat type. By collecting *P. casertanum* in this manner, it was expected that the range in possible forms of this species would be acquired, and that the study would discover some character(s) that could be used to separate all populations of *P. casertanum*

Table 1. Location of populations of *Pisidium* in Ontario, Canada.

Population	Location	Code	Ca[1]	N[2]
P. adamsi				
Carp River	Fitzroy Twp., Carleton Co.	a	230	27
White Lake	Bagot and McNab Twps., Renfrew Co.	b	95	18
P. casertanum				
Aberfoyle Creek	Puslinch Twp., Wellington Co.	c	185	22
Carp River	Fitzroy Twp., Carleton Co.	d	230	33
Golden Lake	North and South Algona Twps., Renfrew Co.	e	34	19
Hanlon Pond	Guelph Twp., Wellington Co.	f	292	25
Yantha Lake	Sherwood Twp., Renfrew Co.	g	44	14
P. compressum				
Carp River	Fitzroy Twp., Carleton Co.	h	230	30
P. subtruncatum				
Carp River	Fitzroy Twp., Carleton Co.	i	230	23

[1] Calcium hardness (mg $CaCO_3l^{-1}$).
[2] Number of clams measured.

from *P. adamsi.*

It is more difficult to identify species of clams with smaller individuals, so all available size classes of clams were represented in the study, when possible (Table 2).

MORPHOMETRIC MEASUREMENTS

All measurements of clams were determined using a binocular microscope equipped with a Bioquant Hipad® digitizer. For measurement of features of the lateral aspect of the shell (Fig. 1A), clams were placed on the right valve in sand such that the dorsal margin was parallel to the first cross-hair (CH1) of the microscope ocular, which went through the most posterior projection of the shell. The second cross-hair (CH2) went through the middle of the umbone. This orientation facilitated measurement of the linear characters A-E and the areas of quadrants 1-4 (Q1-Q4). For the purposes of this study, the point at which the two cross-hairs meet will be termed the centre of the clam. For measurements of the cross-sectional aspect of the shell (Fig. 1B) clams were re-oriented in sand with the anterior end projected upwards, such that the first cross-hair (CH1) went through the maximum width and the second cross-hair (CH2) bisected the two valves. This orientation facilitated measurement of the maximum width and the areas of quadrants 5 and 6 (Q5 and Q6).

The linear measures A-E (Fig. 1A) were taken from the centre of the cross-hairs to the perimeter of the shell along the associated cross-hair. Measurement A provides an estimate of the position of the umbone relative to the posterior margin of the clam. Measurement B estimates the vertical position of the posterior projection relative to the umbone. Measurement C is the maximum distance from the centre of the clam to the shell margin. Measurement D provides an estimate of how "undercut" (Herrington, 1962) the posterior-ventral corner of the shell is; clams that have shorter distances are more undercut. Measurement E provides an estimate of how tapered the anterior-dorsal margin is; clams with shorter distances are more tapered.

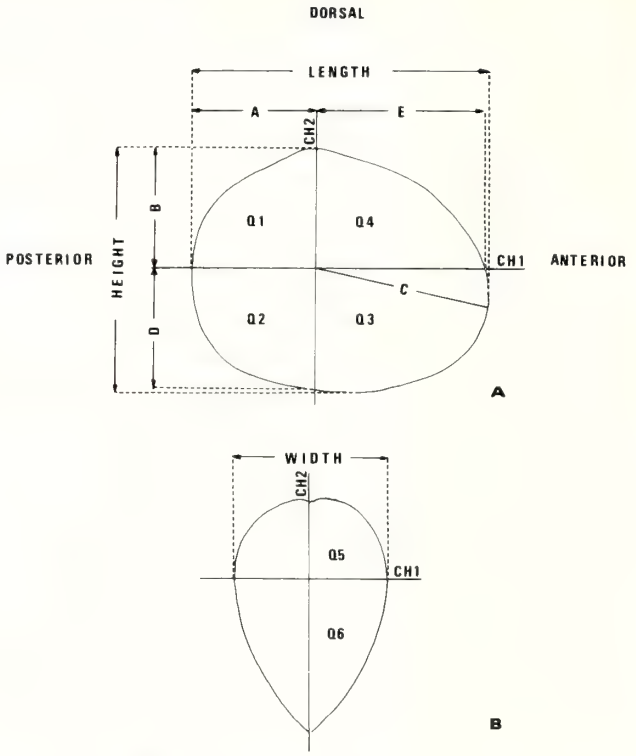

Fig. 1. (A) Lateral view of right valve showing measurements made on each specimen of *Pisidium.* (B) Cross-sectional aspect of the shell, viewed from anterior end, showing measurements made on each specimen. Letters denote measurements: A, distance from umbone to posterior margin; B, distance from centre of the clam to the dorsal margin; C, maximum distance from centre of the clam to the shell perimeter; D, distance from centre of the clam to the ventral margin; E, distance from centre of the clam to the anterior margin; Q1-Q6, quadrants 1 to 6 for which area measurements were made; CH1 and CH2, cross-hairs one and two.

Table 2. Summary of shell length measurements (mm) of nine populations of *Pisidium* from Ontario, Canada.

Population[1]	Minimum	Maximum	Mean	Std Error
a	1.597	4.901	3.042	0.139
b	1.999	4.643	3.273	0.166
c	1.968	5.474	3.640	0.231
d	1.898	4.329	3.387	0.111
e	1.774	3.327	2.563	0.099
f	1.658	3.276	2.538	0.083
g	1.766	5.036	3.172	0.207
h	1.807	3.965	2.854	0.102
i	2.133	4.248	3.337	0.132

[1] See Table 1 for species, location of each population, and sample size.

Estimates of the area of each of the six quadrants were also obtained. These estimates indicate how tapered or rounded a particular quadrant is; clams with a smaller quadrant are more tapered in that quadrant while those with a larger quadrant are more rounded.

STATISTICAL PROCEDURES

Prior to statistical analyses, all data were $\log_{10}$ transformed to improve normality and linearity of relationships. For morphometrics to be useful for classification they must compensate for allometric relationships and be able to separate all size classes of one species from all size classes of other species. For these reasons, each $\log_{10}$ transformed variable was regressed on $\log_{10}$ transformed length. These among-groups residuals (Reist, 1985, 1986) of individual measurements were used to describe shape or morphometric characters of individual clams, and to remove the effects of size. These residuals were then used in all subsequent statistical procedures.

ANOVA and Duncan's multiple range test were performed on the residuals of each measurement to determine if any single characters could be useful for classifying individuals. MANOVA established that signficant differences in population centroids existed ($p < 0.0001$). Since these existed, it justified the use of multiple comparisons techniques (i.e. canonical variates, discriminant functions, and Mahalanobis' distances) to elucidate further morphometric relationships among populations of clams.

Canonical variates analysis (CVA) was used to described axes of variation that provided maximum discrimination among populations of clams (Blackith and Reyment, 1971). Plots of population centroids for each canonical variate and associated 95% confidence ellipses (Altman, 1978) were used to visualize morphometric differences among populations. Canonical variates describing axes of shell variability that accounted for greater than 10% of the variation in the data set and with eigenvalues greater than 0.5 were considered meaningful. Variables with large standardized coefficients (i.e. value of coefficient no smaller than one half the value of the largest coefficient in that variate) and with total canonical structure coefficients greater than 0.5 were considered to be important in determining shell shape in that variate.

Discriminant functions analysis assesses the validity of the group classifications through a jack-knifing technique (Blackith and Reyment, 1971). This technique was used to calcuate discriminant functions for each population of clams. Each individual clam was then re-classified according to these discriminant functions. Clams that were re-classified into their original population were considered correctly re-classified. Those clams re-classified into a different population were considered mis-classified. This analysis effectively assessed the likelihood of making correct classifications using morphometric data. The final procedure was a calculation of Mahalanobis' distances that provided a measure of the morphological distance between groups based on the characters measured (Blackith and Reyment, 1971).

RESULTS

Univariate tests indicated that *Pisidium compressum* and *P. subtruncatum* were significantly different from all other populations with respect to five of the thirteen morphometric characters (Table 3). *P. compressum* from Carp River (population h) were wider, higher, had a lower posterior projection (B) and had larger Q1, Q5, and Q6 than any other population. *P. subtruncatum* from Carp River (population i) had a higher posterior projection (B), longer distance from the centre of the clam to shell margin (C), and had a larger Q3 than any other population.

There were no measurements that could separate all populations of *Pisidium casertanum* from both populations of *P. adamsi*. However, in Carp River, *P. adamsi* (population a) was higher, had a longer distance from the centre of the clam to the shell margin (C), and a smaller Q5 than *P. casertanum* (population d).

There were three meaningful axes of variation described by CVA for shells of *Pisidium* among the nine populations (Table 4). The first canonical variate (CV) described an axis of variation from shells that are low and narrow to shells that are high and wide. The second CV described an axis of variation from shells that have a rounded quadrant 1 (large Q1) and a short anterior-ventral margin (short measurement C) to shells that have a tapered quadrant 1 (small Q1) and a long anterior-ventral margin (long measurement C). The third CV described an axis of variation from shells with a long posterior end (long measurement A) to shells with a short posterior end (short measurement A).

Plots of canonical variate centroids and associated 95% confidence ellipses showed that *Pisidium compressum* (population h) and *P. subtruncatum* (population i) were morphometrically different from each other and from all other populations (Figs. 2-4). *P. adamsi* in Carp River (population a) was significantly different from *P. casertanum* in Carp River (population d) (Fig. 3). Separation of both populations of *P. adamsi* (populations a and b) from all populations of *P. casertanum* (populations b-g) only occurred when canonical variates 1 and 3, or 2 and 3 were considered together (Figs. 3, 4). *P. casertanum* from Golden Lake (population e) were separated from all other populations of *P. casertanum* by canonical variate three (Figs. 3, 4).

From the discriminant functions analysis, 53% of the re-classified clams had a length that exceeded the mean length of the population from which they were originally classified. Over 95% of *Pisidium compressum* (population h) and *P. subtruncatum* (population i) were re-classified correctly (Table 5). The majority of *P. casertanum* were re-classified into their original population or were re-classified into other populations of *P. casertanum*. Only 5.6% of *P. adamsi* from White Lake (population b) were re-classified with the Hanlon Pond population (f) of *P. casertanum*. In contrast, 18.5% of *P. adamsi* from Carp River (population a) were re-classified into populations c and e of *P. casertanum* (Table 5).

Mahalanobis' distances (Table 6) indicated that *Pisidium compressum* (population h) and *P. subtruncatum* (population i) were significantly different, morphometrically, from each other and from all other populations of clams. Also, all populations of *P. casertanum* were significantly different from both populations of *P. adamsi*, except *P. casertanum* from Yantha Lake (population g), which was not significantly different from *P. adamsi* from Carp River (population a).

Table 3. Results of the Duncan's test on shell measurements of nine populations of *Pisidium* in Ontario, Canada. Population means sharing the same letter superscript in the same row are not signifying different ($p<0.05$). Analysis is based on residuals of 13 morphometric measurements after variation due to shell length was removed. Refer to text for explanation of abbreviations.

Variable	Population[1]								
	a	b	c	d	e	f	g	h	i
Height	0.0006^{vw}	-0.005^{wx}	-0.012^{xy}	-0.013^{y}	0.006^{v}	-0.010^{xy}	-0.006^{wxy}	0.038^{u}	-0.008^{xy}
Width	-0.010^{wxy}	-0.026^{yz}	-0.016^{wxyz}	-0.003^{w}	0.020^{v}	-0.021^{xyz}	-0.007^{wx}	0.069^{u}	-0.028^{z}
A	0.003^{vw}	0.019^{u}	-0.004^{w}	0.004^{v}	-0.014^{x}	0.007^{v}	0.004^{v}	-0.001^{vw}	-0.017^{x}
B	-0.009^{wx}	-0.022^{x}	-0.007^{wx}	-0.010^{wx}	0.025^{v}	0.001^{w}	0.007^{w}	0.049^{u}	-0.041^{y}
C	0.003^{vw}	-0.013^{y}	-0.002^{wx}	-0.005^{w}	0.005^{v}	-0.011^{y}	-0.008^{xy}	0.008^{v}	0.019^{u}
D	0.001^{u}	-0.006^{u}	-0.005^{u}	0.002^{u}	-0.010^{u}	-0.009^{u}	-0.001^{u}	0.012^{u}	0.007^{u}
E	-0.006^{uvw}	-0.014^{vw}	0.006^{uv}	0.019^{u}	0.013^{u}	0.004^{uv}	0.005^{uv}	-0.026^{w}	0.001^{uv}
Q1	-0.012^{w}	0.008^{v}	-0.012^{w}	-0.001^{vw}	0.004^{vw}	0.011^{v}	0.010^{v}	0.032^{u}	-0.044^{x}
Q2	0.011^{v}	0.041^{u}	-0.016^{vw}	-0.005^{vw}	-0.024^{w}	-0.003^{vw}	-0.005^{vw}	0.013^{v}	-0.010^{vw}
Q3	-0.001^{w}	-0.009^{wx}	-0.021^{wx}	-0.017^{wx}	0.001^{w}	-0.030^{x}	-0.023^{wx}	0.033^{v}	0.056^{u}
Q4	0.011^{uv}	0.001^{uv}	0.028^{uv}	-0.030^{vw}	0.046^{u}	0.029^{uv}	0.031^{uv}	-0.005^{uv}	-0.078^{w}
Q5	-0.038^{xy}	-0.080^{y}	0.018^{vw}	0.015^{w}	0.061^{uv}	-0.015^{wx}	0.013^{w}	0.077^{u}	-0.073^{y}
Q6	-0.014^{w}	-0.020^{w}	-0.029^{w}	-0.021^{w}	0.025^{v}	-0.031^{w}	-0.018^{w}	0.113^{u}	-0.034^{w}

[1] See Table 1 for species, location of each population, and sample size.

Table 4. Standardized and total structure coefficients for shell morphometric data from nine populations of *Pisidium* in Ontario, Canada. Analysis is based on residuals of 13 shell morphometric measurements after variation due to shell length was removed. The eigenvalue and the proportion of variance accounted for by a particular variate are also presented. Refer to text for explanation of abbreviations.

Variable	Canonical Variate					
	Standardized Coefficients			Total Structure Coefficients		
	CV1	CV2	CV3	CV1	CV2	CV3
height	1.203	-1.680	-1.134	0.932	-0.028	0.096
width	0.712	-0.121	0.437	0.854	0.158	0.391
A	0.334	0.190	-0.869	0.007	0.452	-0.760
B	-0.269	1.727	0.714	0.654	0.440	0.331
C	0.147	-1.053	0.056	0.261	-0.733	0.453
D	0.154	-0.126	-0.171	0.129	-0.122	0.011
E	-0.345	0.209	0.223	-0.338	0.097	0.267
Q1	0.150	-0.870	-0.120	0.438	0.521	-0.093
Q2	-0.050	0.340	0.141	0.133	-0.006	-0.460
Q3	0.014	-0.203	0.102	0.324	-0.640	0.129
Q4	0.086	0.252	-0.203	0.022	0.350	0.024
Q5	-0.190	0.327	0.464	0.389	0.362	0.568
Q6	0.290	0.278	0.154	0.846	0.060	0.216
eigenvalue	3.016	1.502	0.745			
% variance	0.534	0.265	0.132			

DISCUSSION

SEPARATING SPECIES OF *PISIDIUM*

Size of clams used does not appear to have affected the results of this study. Greater than 50% of the misidentified clams, from the jack-knifed classification, were larger than the average-sized clams. This suggests that small clams can be used in a study of this type without resulting in appreciable size-related bias.

The morphometric measurements that have been described in this study appear to be useful for separating species of *Pisidium*. Both univariate and multivariate statistical techniques were successful at separating *P. compressum* and *P. subtruncatum* from each other and from *P. adamsi* and *P. casertanum*. In the future, these new measurements, coupled with adjustments for shell length (i.e. generation of residual values after length variation is removed), could be useful for objectively describing shell shape to identify other species of *Pisidium*.

In addition to being useful for classifying species with unique forms, these morphometric data appear to be useful for separating populations of the same species. For example, plots of canonical variate ellipses suggests that *P. casertanum* from Golden Lake (population e) have significantly different forms when compared to other populations of *P. casertanum*.

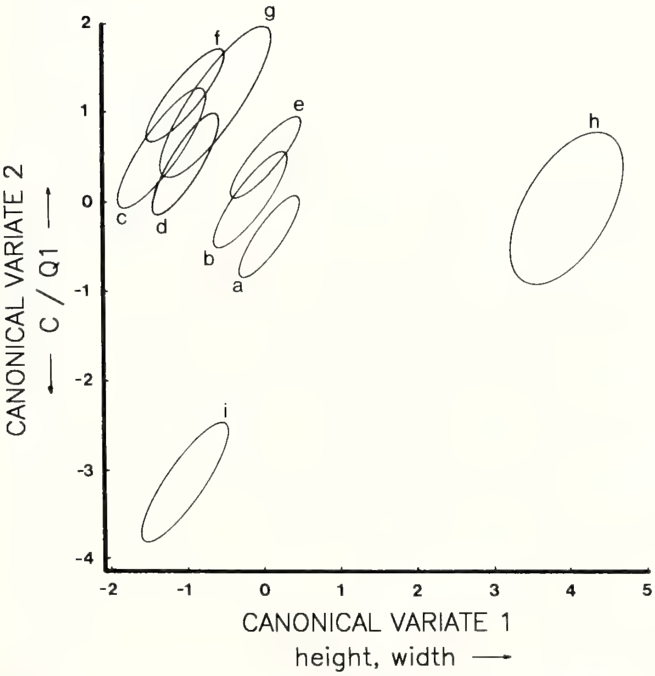

Fig. 2. Plot of centroids for canonical variates 1 and 2, with 95% confidence ellipses for 9 populations of *Pisidium* in Ontario, Canada. Letters denote populations: a and b, *P. adamsi*; c-g, *P. casertanum*; h, *P. compressum*; i, *P. subtruncatum*. Arrows indicate direction in which the variables increase. Refer to text for explanations of abbreviations of morphometric variables.

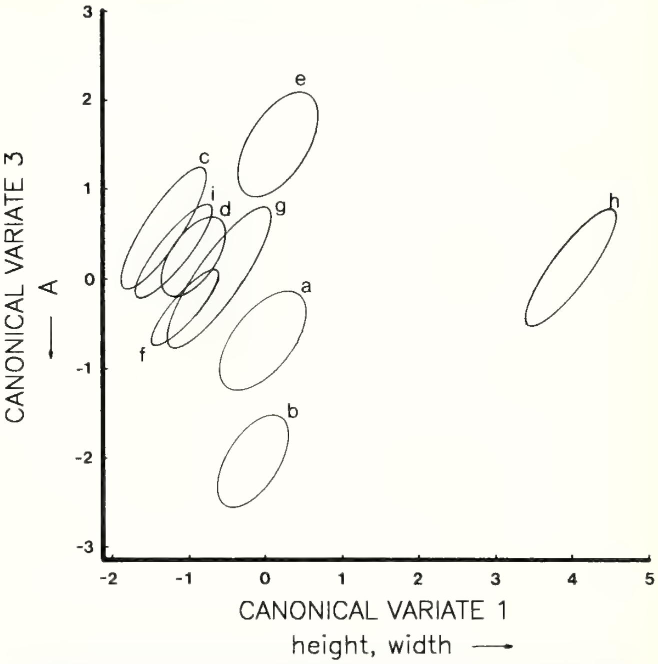

Fig. 3. Plot of centroids for canonical variates 1 and 3, with 95% confidence ellipses for 9 populations of *Pisidium* in Ontario, Canada. Letters denote populations: a and b, *P. adamsi*; c-g, *P. casertanum*; h, *P. compressum*; i, *P. subtruncatum*. Arrows indicate direction in which the variables increase. Refer to text for explanations of abbreviations of morphometric variables.

SEPARATING *PISIDIUM ADAMSI* AND *P. CASERTANUM*

The analysis showed that *Pisidium adamsi* and *P. casertanum* have unique forms but it is difficult to make confident classifications for all clams using morphometric data. Also, *P. adamsi* and *P. casertanum* are more easily distinguishable when compared within a habitat than among habitats. For example, univariate tests showed that *P. adamsi* and *P. casertanum* from Carp River (populations a and d respectively) can be distinguished from each other using morphometric data. However, there were no single measurements that could separate both populations of *P. adamsi* from all populations of *P. casertanum*. Plots of canonical variate ellipses showed that, in general, *P. adamsi* have a longer posterior end, a more tapered Q1 and are higher. However, discriminant functions analysis showed that although most clams can be correctly classified (e.g. *P. casertanum* from Aberfoyle Creek and Golden Lake were correctly re-classified as *P. casertanum* 100% of the time), there are some clams (e.g. *P. adamsi* from White Lake were incorrectly re-classified as *P. casertanum* 18.5% of the time) that are difficult to classify using morphometric data (Table 5). As well, Mahalanobis' distances showed that the Yantha Lake population of *P. casertanum* (population g) is not morphometrically distinct from either *P. casertanum* or *P. adamsi* populations from Carp River (populations d and a respectively), suggesting that there are forms that could be mistaken for either of *P. adamsi* or *P. casertanum* using morphometric data. It is not reliable, therefore,

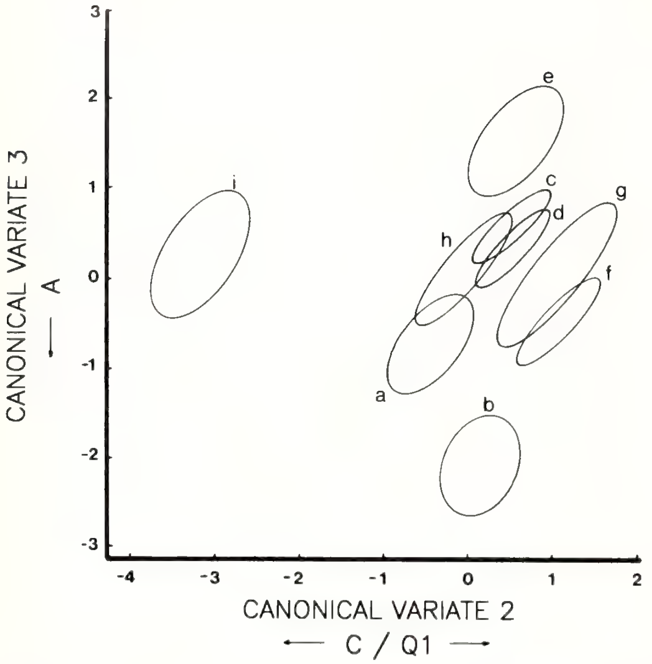

Fig. 4. Plot of centroids for canonical variates 2 and 3, with 95% confidence ellipses for 9 populations of *Pisidium* in Ontario, Canada. Letters denote populations: a and b, *P. adamsi*; c-g, *P. casertanum*; h, *P. compressum*; i, *P. subtruncatum*. Arrows indicate direction in which the variables increase. Refer to text for explanations of abbreviations of morphometric variables.

to use shell morphometric data to separate *P. adamsi* and *P. casertanum*.

Although these data show that the morphometric measurements described here are useful for making a less subjective classification of some species of *Pisidium*, some species such as *P. adamsi* and *P. casertanum* require additional information. In other molluscs, classification has been

Table 5. Jack-knifed classification, using shell measurements, of nine populations of *Pisidium* in Ontario, Canada. Analysis is based on residuals of 13 shell morphometric measurements after variation due to shell length was removed first. Values in parentheses refer to the proportion of mis-classified clams made into each of the indicated populations.

Species	Population[1]	% correct	% clams mis-classified in other population
P. adamsi	a	59.3	b (18.5), c (7.4), e (11.1), i (3.7)
	b	77.8	a (16.7), f (5.6)
P. casertanum	c	59.1	d (18.2), e (9.1), f (9.1), g (4.6)
	d	44.5	a (6.1), c (18.2), 3 (3.0), f (12.1), g (9.1), i (6.2)
	e	84.2	c (10.5), g (5.3)
	f	48.0	b (8.0), c (4.0), d (4.0), e (4.0), g (32.0)
	g	28.6	b (7.1), c (7.1), d (14.3), e (14.3), f (28.6)
P. compressum	h	96.7	g (3.3)
P. subtruncatum	i	95.7	a (4.3)

[1] See Table 1 for location of each population and sample size.

Table 6. Mahalanobis' distances, using shell measurements, between populations of *Pisidium* in Ontario, Canada. Analysis is based on residuals of 13 shell morphometric measurements after variation due to shell length was removed.

Population[1]	b	c	d	e	f	g	h	i
a	* 1.94	** 2.24	** 2.18	** 2.67	** 2.18	ns 1.99	** 4.16	** 3.24
b		** 3.05	** 2.81	** 3.68	** 2.28	** 2.48	** 4.70	** 4.17
c			ns 1.50	** 2.05	ns 1.35	ns 1.20	** 5.40	** 3.78
d				** 2.25	* 1.60	ns 1.37	** 5.10	** 3.73
e					** 2.45	** 1.98	** 4.21	** 4.20
f						ns 0.72	** 5.24	** 4.38
g							** 4.75	** 4.27
h								** 5.40

[1] See Table 1 for species, locations of each population, and sample size.
* = Populations are significantly different at $P < 0.05$.
** = Populations are significantly different at $P < 0.01$.
ns = Populations are not significantly different.

improved through study of soft part anatomies (e.g. Davis and da Silva, 1984; Dillon, 1984; Kat, 1983). It would be beneficial if more detailed studies of the morphologies of *P. adamsi* and *P. casertanum* could be performed so that more reliable means of classification be determined. Also, similar shell morphometric studies on all species of Sphaeriidae are needed before the use of shell morphometric measurements can be fully assessed.

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POLYMORPHISM FOR SHELL COLOR IN THE ATLANTIC BAY SCALLOP *ARGOPECTEN IRRADIANS IRRADIANS* (LAMARCK) (MOLLUSCA:BIVALVIA) ON MARTHA'S VINEYARD ISLAND

J. A. ELEK[1] AND **S. L. ADAMKEWICZ**
GEORGE MASON UNIVERSITY
FAIRFAX, VIRGINIA 22030 U.S.A.

ABSTRACT

Populations of the Bay Scallop, *Argopecten irradians irradians* (Lamarck, 1819) on the island of Martha's Vineyard, Massachusetts, are highly polymorphic for shell colors and patterns. Juvenile and adult scallops were sampled from natural populations in two ponds on the island and a system was devised for classifying the wide range of variation found in their shell colors and patterns. This classification, which we propose as a guide for future genetic analysis, recognizes three background colors (white, yellow, and orange) and six overlying colors that contribute to a variety of patterns. Frequencies for some of these shell characters differ significantly between ponds and sometimes between age classes within a pond. For background color, approximately 94% of the entire sample were white, 5% were yellow, and 1% were orange. This polymorphism, which is known to be genetic with rare yellow and orange alleles dominant to white, appears to be persistent and can be maintained by frequency dependent selection through predation by teleost fish and shore birds. The entire suite of polymorphic shell characters could be an instance of hyperpolymorphism maintained by reflexive selection.

Scallops are renowned for their brilliant shell colors, but few studies have investigated this characteristic. Abbott (1954) described the occurrence of several different colors in shells of the bay scallop *Argopecten irradians irradians* (Lamarck, 1819). Clarke (1965) also noted that various shell colors existed in this species. Using museum collections, he estimated the frequency of shells with white lower valves in populations along the Atlantic coast of North America and showed that significant differences occur for this pattern variant. Clarke (op. cit.) also remarked that only white shells occurred in frequencies high enough to record. Kraeuter *et al.* (1984) first produced evidence, by using mass spawnings, that shell colors in *A. i. irradians* were independent of the environment, and Adamkewicz and Castagna (1988) have shown that background color in these scallops is inherited as a single gene with orange and yellow alleles dominant to white. Their work has demonstrated the need of a system for classifying the shell colors to facilitate planning and interpretation of further breeding experiments and to permit systematic observation of natural populations.

Many marine mollusks are highly polymorphic and researchers have investigated whether their shell colors were determined by genetic or environmental factors. Environmental control of shell color has been proposed for the gastropods *Turbo cornutus* Lightfoot (Ino, 1949), *Haliotis rufescens* Swainson (Leighton, 1961), and *Austrocochlea constricta* Lamarck (Creese and Underwood, 1976) as well as for the clam *Donax denticulatis* Linné (Wade, 1968). If most such polymorphisms had an environmental cause, then they would not be suitable for studies of natural selection. However, several investigators have now succeeded in demonstrating a genetic basis for variations in shell color in marine mollusks, and some studies have linked these variations to differential survival.

Geisel (1970) and Reimchen (1979) have described situations where variations in shell color of the limpet *Acmea digitalis* Rathke and the snail *Littorina mariae* Philippi respectively, which had appeared to be related to environmental factors, were actually polymorphisms maintained by selective predation. A genetic basis for shell color has now been demonstrated in the mussel, *Mytilus edulis* Linné (Innes and Haley, 1977) and the color variants have been shown to differ in growth rate (Newkirk, 1980) as well as in resistance to high temperatures (Mitton, 1977). Cole (1975) has shown that, although it can change during growth under the influence of environmental factors such as diet, shell color in the gastropod *Urosalpinx cinerea* Say is inherited directly. Palmer (1985) has demonstrated that a single gene determines shell color in the snail *Thais (=Nucella) emarginata* Deshayes while Etter (1988) has shown a relationship between shell color and survival at high temperatures in the snail *Nucella lapillus* Linné.

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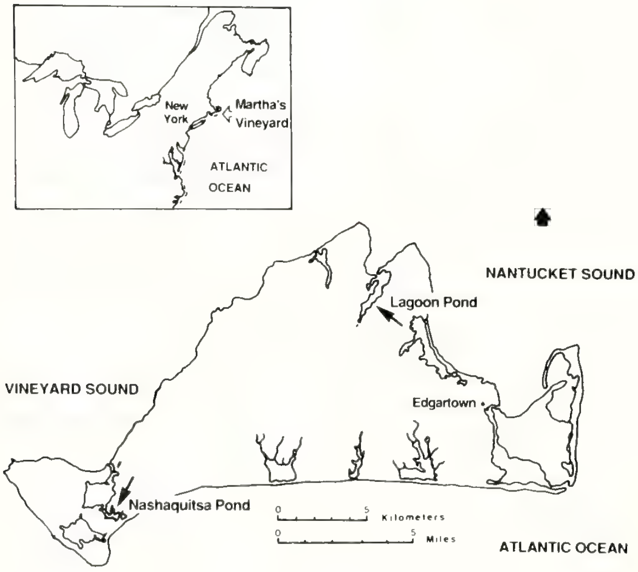
[1] Present address: CSIRO, Division of Entomology, P.O. Box 1700, Canberra City, ACT, Australia, 2601.

The present study was designed to ascertain the extent of polymorphism in the scallop *Argopecten irradians irradians* and the suitability of the variation for ecological and evolutionary studies. We propose a system for classifying the very extensive variation observed into a manageable number of discrete categories or phenotypes. This system has been used to estimate proportions of these phenotypes in natural populations from Martha's Vineyard Island, Massachusetts, and to compare phenotypic frequencies both between populations from two different ponds and between adults and juveniles within a single pond. Although the forces acting on this polymorphism are not yet known, the system appears promising for future study.

MATERIALS AND METHODS

STUDY AREA

The island of Martha's Vineyard (Fig. 1) is situated 13 km south of Cape Cod, Massachusetts, at 40°N, 70°W. It is approximately 32 km long and 14 km wide with numerous large estuarine ponds which support extensive shellfish beds. Samples were taken from two of these ponds, Lagoon and Nashaquitsa. Lagoon Pond is on the north shore of the island and covers about 236 hct with a narrow opening into Vineyard Haven Harbour. Its salinity ranges from 22 to 34 ppt during the year, and the seaward portion has numerous scallop beds. Nashaquitsa Pond covers about 40 hct and, although it is on the southwest side of the island, it connects through Menemsha Pond to Vineyard Sound on the northwestern shore. Salinity ranges between 26 and 35 ppt. Despite its poor water circulation, the scallop beds are very productive.



Martha's Vineyard

Fig. 1. Map of Martha's Vineyard showing the locations of the two ponds and the position of the island relative to the eastern coast of the United States.

Because it was not feasible to sample the ponds randomly, four sampling sites were chosen from each pond to represent, so far as possible, the range of variation in physical parameters such as depth, salinity and distance from the outlet. Sites in both ponds ranged from 0.5 to 2 m in depth, salinity was from 32 to 33 ppt, and water temperature was 13°C in Nashaquitsa Pond and 13° to 15°C in Lagoon Pond at time of sampling in May 1984. The substrata at three of the four sites in each pond consisted of mud with eelgrass and algae (*Gracillaria* sp. and *Codium* spp.). One site in Nashaquitsa Pond was muddy with many dead shells, while one site in Lagoon Pond was sandy and also had many dead shells.

SAMPLING AND SHELL PREPARATION

The scallops were collected by dredging four sites in each pond. This produced a sample of 302 adults from Lagoon Pond and 310 adults from Nashaquitsa Pond. The soft parts were removed and the shells were soaked in strong detergent, then scrubbed to remove light fouling. A few shells were soaked in diluted bleach for about 15 min to remove more persistent fouling, but this treatment did not affect the underlying shell material or color. Finally, the shells were sprayed with clear acrylic to restore their "wet" appearance. During the summer of the same year, juvenile scallops were sampled by means of spat collectors, synthetic mesh bags which provided setting sites for the scallop larvae. Bags were suspended at one site in each pond for the three summer months of June, July and August. When removed at the end of August, the bags from Lagoon Pond contained 231 juvenile scallops and the bags from Nashaquitsa Pond yielded 371. Because no fouling organisms had settled on them, the young scallops required no cleaning to reveal shell colors.

Each shell was measured with calipers to the nearest 0.1 mm while the two valves were held closed. Three dimensions were measured as follows: height, greatest distance from hinge to growing edge, usually taken along the middle rib; width, greatest distance across ribs, at right angles to the middle rib; depth, greatest distance through the shell from top to bottom valve. For the shells of adults, the measurements of height and depth were combined to produce an index expressing the degree of curvature of the valves as follows: relative depth = depth/height.

The classification system for shell color was devised from a preliminary sample of 250 adult shells taken from a third pond on Martha's Vineyard in May of 1983. Reference shells were selected for each of the colors and patterns to standardize classification of shell phenotypes, and these reference shells are held at George Mason University with one of the authors (S.L.A.). [A selection of these shells can be seen in color photographs in Elek (1985) and Adamkewicz and Castagna (1988)].

Because the top and bottom valves differ markedly in the distribution of pigments, phenotypes were recorded as either present or absent separately for the top and bottom valves of each scallop collected. Intensity of pigmentation was not recorded at all due to the difficulty of making objective measurements, and extent of coverage on the shell was recorded only qualitatively. The patterns and colors on each adult shell were assessed separately in three zones which corresponded to the length of early juveniles that attach to eel grass and other raised locations (about 5 mm), of late juveniles that release from the eel grass to settle on the bottom (about 20 mm), and of fully adult scallops that have stayed on the pond bottom resting on their lower (right) valves for nearly a year (over 40 mm).

All statistical analyses were performed using the Statistical Package for Social Science (SPSS) Version 9 (Nie *et al.,* 1975). Contingency tests were used to search for significant variation among phenotypic frequencies and analysis of variance was used to test for significant differences in shell size among the various phenotypes. A result was considered significant when the probability of its occurrence was less than 0.05 and was considered highly significant when the probability was less than 0.01.

RESULTS

CLASSIFICATION OF SHELL COLOR AND PATTERN

The overall appearance of the shell depends on three factors which are summarized with their individual variants in Table 1. These factors, the background color of the shell, the pattern applied over this ground color, and the color(s) used to produce the patterns, are definitely not independent of one another in their occurrence, and only for background color is the genetic basis known. The analysis of the patterns and their colors is further complicated because these two factors have a strong developmental component. Both the interactions and the developmental sequence will be described after the basic variants of the factors and their frequencies have been presented.

Background color is defined as the color which suffuses both valves of the shell and which is produced uniformly throughout the life of the animal (i.e. intensity does not vary). Three background colors were identified which were mutually exclusive in their occurrence: 1) white, probably an absence of pigment; 2) yellow, ranging in intensity from cream to golden; 3) orange, also varying in intensity. Scallops always had one of the three alternative background shell colors, the same on both valves.

Pattern colors are pigments overlying the background color and not covering the entire shell. Unlike background color, pattern colors are not alternatives and can be different on top and bottom valves. Six different colors were identified which could occur either separately or in any combination with one another and could overlay any of the three background colors. These pattern colors were further subdivided according to whether the pigment could cover large areas of the shell or could occur only episodically as small markings. The three episodic pigments are white, gray, and yellow. White, an opaque pigment distinct from the white background color usually occurs as mottles or chevrons. Based on a microscopic examination of the shell, this color appears definitely to be an applied pigment and not an absence of pigment. The pale dove gray can merge into the white pigment and can be a variant of it. This color often overlays slate and brown. Yellow appears to be similar to background yellow, but, unlike background, its coverage and intensity were not uniform on a single shell. The three covering pigments, which can occur mixed on the same shell, are: 1) slate, a dark greeny-gray color which varied little in intensity; 2) brown, a chocolate color ranging from pale to very dark; 3) chestnut, an orangish to reddish brown which could vary in intensity. Because the overall appearance of the shell was so strongly affected by whether or not the covering pigment was chestnut, scallops could be assigned to one of two "overall appearance" categories, "chestnut present" and "chestnut absent", regardless of other factors.

Table 1. Summary of the system used to describe and classify the appearance of the shell.

Factor		Variants
Background Color		white yellow orange
Pattern Color	episodic	white gray yellow
	covering	slate brown chestnut
Pattern	episodic	bands rays mottle & chevron
	covering	continuous ribs only top valve only
Overall Appearance		chestnut present chestnut absent

Patterns, as shown in figure 2, can be of several different types which are not necessarily genetically related to one another. Like the pigments, they have been subdivided into episodic patterns, which can occur on shells of any background color, and overall patterns, which occur only on white shells. *Argopecten irradians irradians* is usually regarded as having a dark shell, but this is only because the commonest phenotype is a white shell with an overall pattern of dark pigment.

There are three episodic patterns: "bands", "rays", and "mottle & chevron". "Bands" are strips of brown or chestnut laid down parallel to the growing edge of the shell (Fig. 2a and 2b, bottom valve; Fig. 2d, top valve). They are produced by episodic production of pigment as the shell grows. "Rays" are produced by a lack of pigment along one or more of the shell's ribs from hinge to lip (Fig. 2e). This is a failure to produce pigments in a particular sector of the mantle edge. In nature we have seen rays only on white shells with dark overall patterns. However, scallops bred in a hatchery (Kraeuter

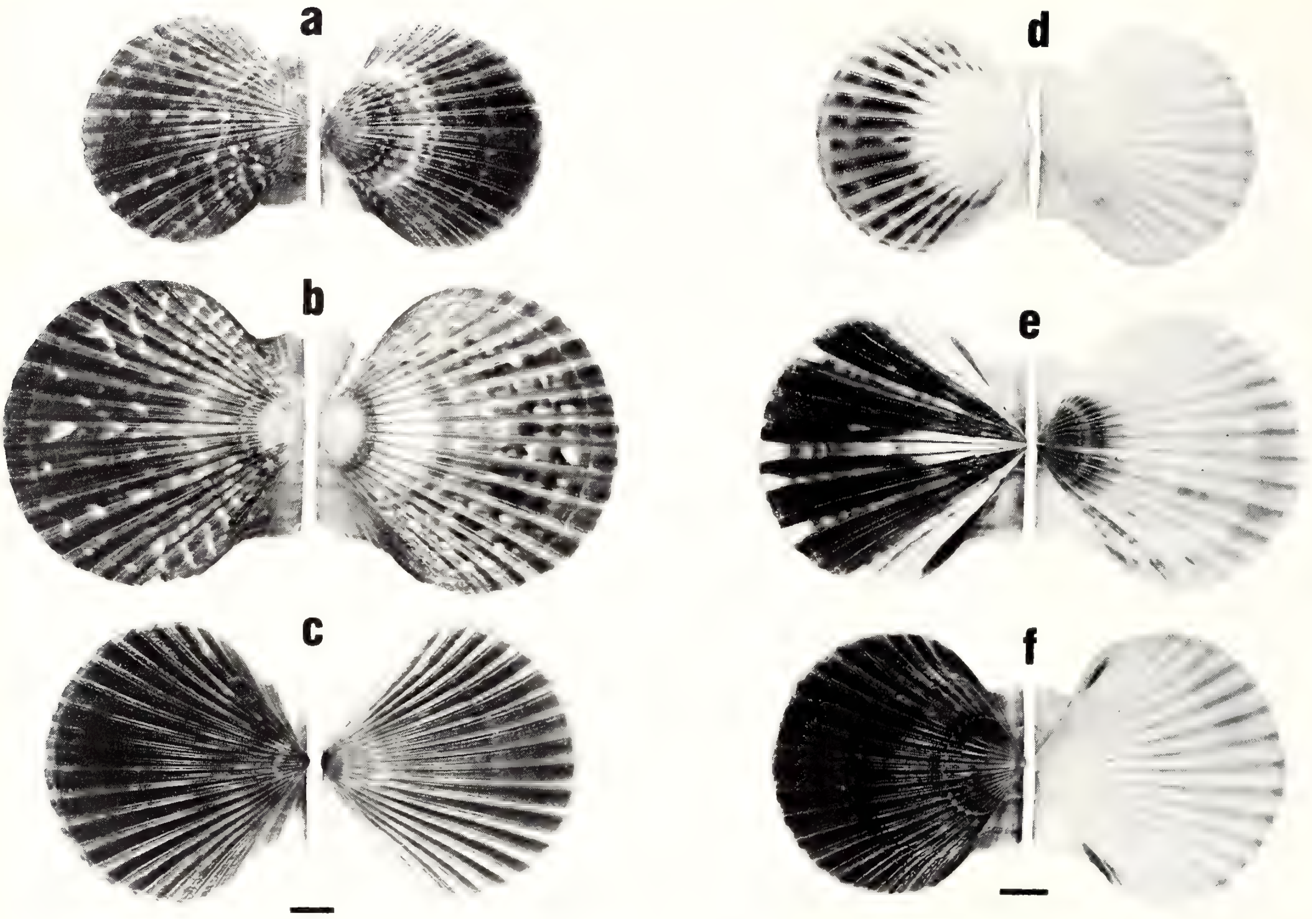


Fig. 2. Photographs of six scallops that exemplify the various patterns described in the text. For each shell, the top (left) valve is to the left and the bottom (right) valve, with its distinctive byssal notch, is to the right. Top and bottom valves show different patterns as follows: a) upper- continuous with mottle, lower- continuous with bands; b) upper- continuous with chevrons, lower- continuous with mottles; c) upper- continuous, lower- ribs only; d) upper- bands on ribs only, lower- no pigments; e) upper- continuous with rays, lower- unmarked except in juvenile region which is continuous; f) upper- continuous, lower- no pigments (scale bars = 1 cm).

et al., 1984) have had white (presumably unpigmented) rays on shells with orange or yellow background. "Mottle & chevron" are white, gray, or sometimes yellow markings that are caused by the active, episodic secretion of a light pigment, not by an absence of color. They occur only scattered across one of the covering patterns. Mottles (Fig. 2a, top valve; Fig. 2b, bottom valve) are rectangular patches of pale pigment usually limited to a section of one rib while chevrons (Fig. 2b, top valve) are "V"-shaped and often extend across several ribs. Whether these two have different causations is not known, and they are grouped in this analysis as "mottle & chevron".

There are three covering patterns: "continuous", "ribs only", and "top valve only". In the "continuous" pattern the entire valve can be covered with dark pigment so that only close examination of the auricles will reveal that the background color is white (Fig. 2c and 2f, top valves). In "ribs only" the continuous pigment can occur only on the tops of the ribs and not in the furrows (Fig. 2c, bottom valve). This gives the shell a rayed appearance that is very regular and distinct from the episodically rayed pattern. A banded shell can also show this pattern (Fig. 2d, top valve) because those areas banded with dark pigment can have it on the tops of ribs only or on both rib and furrow. In "top valve only" the continuous pigment, whether marked with an episodic pattern or not, is sometimes restricted to the top valve only (Fig. 2f) or to the top valve and the juvenile portion of the bottom valve (Fig. 2e).

FREQUENCIES OF SHELL PHENOTYPES

All the adult and juvenile scallops collected from Lagoon and Nashaquitsa ponds were scored for appearance of the shell using the classification system described above. The four adult samples from each pond were first tested for homogenity of frequencies and then pooled to estimate phenotypic frequencies for that pond, while the juveniles from all the spat collectors in one pond were treated as a single sample. Three main analyses were then performed. First, comparisons were made between the two age classes within

Table 2. Frequencies of the three background colors on juvenile and adult shells from Lagoon and Nashaquitsa Ponds. Using contingency chi squares, like age classes were compared between ponds and different age classes within ponds.

	Lagoon Pond		Nashaquitsa Pond	
Color	Juvenile	Adult	Juvenile	Adult
White	0.870	0.950	0.976	0.952
Yellow	0.113	0.033	0.024	0.039
Orange	0.017	0.017	0.000	0.010
N	231	302	371	310

Results of Contingency Tests (in all cases, degrees of freedom = 1):

Between ponds	- Juveniles:		$X^2 = 5.03$ $p < 0.0001$
	- Adults:		$X^2 = 0.58$ $p > 0.4$ ns
Between ages	- Lagoon Pond:		$X^2 = 13.15$ $p < 0.0003$
	- Nashaquitsa Pond:	chi	$X^2 = 5.03$ $p < 0.03$

Table 3. Frequencies of the two types of overall appearance on juvenile and adult shells from Lagoon and Nashaquitsa Ponds.

	Lagoon Pond		Nashaquitsa Pond	
Color	Juvenile	Adult	Juvenile	Adult
Chestnut Absent	0.898	0.868	0.865	0.805
Chestnut Present	0.102	0.132	0.135	0.195
N	231	302	371	310

Results of Contingency Tests (in all cases, degrees of freedom = 1):

Between ponds	- Juveniles:		$X^2 = 1.20$ $p > 0.25$ ns
	- Adults:		$X^2 = 4.78$ $p < 0.03$
Between ages	- Lagoon Pond:		$X^2 = 1.00$ $p < 0.31$ ns
	- Nashaquitsa Pond:	chi	$X^2 = 4.60$ $p < 0.03$

each pond to investigate whether frequencies changed with age. Second, the same age classes were compared between ponds to estimate the extent of variation between populations. Third, the occurrences of pattern color phenotypes were tested for positive or negative associations that might suggest underlying genetic relationships.

Table 2 shows that, although yellow and orange are definitely variants of a genetic polymorphism, their frequencies were low in all groups. Frequencies of the colors in the two adult samples were homogeneous and indistinguishable. However, juvenile scallops differed from adults in each pond and juveniles from Lagoon Pond had a significantly higher proportion of yellow shells compared with juveniles from Nashaquitsa. Results were also significant when frequencies of the two "overall appearance" morphs, "chestnut present" and "chestnut absent" were compared (Table 3), but here the deviant groups are adults in Nashaquitsa and juveniles in Lagoon Pond.

Table 4 summarizes the data for four of the shell patterns. Comparisons of pattern frequencies using contingency chi squares showed different results for each character. The frequencies of shells with "ray" pattern were homogeneous both between age groups and between ponds, while the frequencies of "ribs only" differed significantly between age groups but not between ponds. The frequencies of "mottle & chevron" and "top valve only" differed significantly both between age groups and, for adults only, between ponds, both being significantly more frequent among adults in Nashaquitsa than in Lagoon Pond.

A comparison of the two ponds, by valve, for the frequencies of individual pattern colors on the adult shells (Table 5) revealed more consistent differentiation between the two ponds, with all but three of the paired comparisons (yellow on top valves, brown and white on bottom valves) showing significant differences between the ponds. Juveniles were not included in this analysis because their shells might not have had time to develop all their colors. Brown was the most common color in both ponds and chestnut the least common. Note that all the dark covering pigments were more common on the top than on the bottom valves, as was the episodic pigment white, which was associated with the dark colors through the pattern "mottle & chevron". This is a quantitative expression of the qualitative observation that the top valve of adults always appears darker than the bottom valve.

To investigate whether the occurrences of different colors were associated, and, if so, whether the association was positive or negative, the six pattern colors were tested for independence in all possible pairs using 2x2 contingency chi squares, presence/absence of one color in the sample versus presence/absence of the other color. Only adult scallops were included because of the possibility that juveniles had not yet developed all of their adult coloration. For any significant chi square, the degree of association was assessed by the contingency coefficient, Phi = X^2/N, with values ranging

Table 4. Frequencies of the various patterns on juvenile and adult shells from Lagoon and Nashaquitsa Ponds. For each age class in each pond, the total number of animals counted is the same as shown in Table 3. Contingency tests were performed between age classes in one pond and between the same ages in the two ponds with results as discussed in the text.

	Juvenile		Adult	
	Top	Bottom	Top	Bottom
Rays				
Lagoon	0.048	-0-	0.043	0.020
Nashaquitsa	0.050	0.011	0.042	0.019
Mottle & Chevron				
Lagoon	0.865	0.790	0.689	0.180
Nashaquitsa	0.897	0.850	0.858	0.300
Ribs only:				
Lagoon	0.033	0.511	0.060	0.745
Nashaquitsa	0.111	0.510	0.033	0.652
Top valve only:				
Lagoon	—	—	0.510	
Nashaquitsa	—	—	0.558	

Table 5. Frequencies of individual pattern colors on both top and bottom valves of adult shells from Lagoon and Nashaquitsa Ponds. Note that multiple colors can appear on one shell. In contingency comparisons of the same valve between ponds, all comparisons were significantly different at the 0.05 level except as noted (*).

	Covering Colors			Episodic Colors			
	Chestnut	Slate	Brown	White	Gray	Yellow	N
Lagoon Pond							
Top	0.13	0.93	0.95	0.24	0.80	0.57*	302
Bottom	0.13	0.55	0.89*	0.05*	0.47	0.71	302
Nashaquitsa Pond							
Top	0.19	0.88	0.91	0.78	0.56	0.63*	310
Bottom	0.19	0.46	0.85*	0.09*	0.35	0.80	310

from 0 (not associated) to 1 (perfectly associated). The results (Table 6) are not shown separately for top and bottom valves because the associations between the colors were the same on both valves. With two exceptions (the associations between white/brown and yellow/gray were significant in one pond but not the other) the 15 comparisons gave the same results in both ponds. The patterns of association, with very negative associations of chestnut with brown, yellow, and gray and a correspondingly strong positive association of brown with yellow and gray, support the reality of the variants for "overall appearance" based on presence or absence of chestnut. Strong positive associations also exist for slate with white and slate with gray, while slate itself shows no association with chestnut and only a modest association with brown.

Table 7 summarizes the results for shell dimensions. Measurements of the same age classes were compared between ponds using a one way analysis of variance, and both juveniles and adults from Lagoon Pond were significantly larger in all linear dimensions than the same age groups from Nashaquitsa Pond. Although relative depth was not tested for significance, adult shells from Nashaquitsa did have more strongly curved valves, as indicated by a greater value for relative depth. There was no significant difference in size associated with any pattern or color except for presence/absence of chestnut. Shells with chestnut pigment were on average 2 mm smaller in height and width than shells without chestnut but were slightly deeper.

DISCUSSION

Argopecten irradians irradians exhibits a wide range of variation in the patterns and colors of its shells. The system proposed in this study classifies this variation into three background colors, six pattern colors, and six patterns. These categories have the virtue of being discrete, with only two or three alternatives each, which leads to testable genetic hypotheses. The significant positive and negative associations among the six pattern colors suggest that the underlying pigments can be a sequence of products in one, or a few, biochemical pathways. Background color is already known to behave as a single gene trait, and it is reasonable to believe that the pattern colors will also be shown to be under the control of only a few genes.

The patterns themselves present a more complicated picture, with expression influenced by both genetic and environmental factors. The genetic interaction is clearly shown by the results of earlier breeding experiments (Adamkewicz and Castagna, 1988) in which self-fertilized crosses of uniformly orange (or yellow) scallops produced offspring of two kinds, those with orange background (or yellow) and those with white background, in the standard 3:1 Mendelian ratio. Although the parents had unpatterned valves, the patterns “mottle & chevron” and “top valve only” did appear in the offspring, indicating recessive inheritance of these patterns. However, the patterns occurred only on the one-quarter of the offspring with white background color, never on the three-quarters of the offspring with orange or yellow backgrounds. In the natural population also, we never observed the patterns “mottle & chevron” or “top valve only” on scallops with orange or yellow background color. Yellow and orange shells can be extensively covered with dark pigments, but not in a “mottle & chevron” pattern. These observations support a model in which one or more genes determine pattern, and these gene(s) either interact in recessive epistasis with the gene for background color or perhaps are held in a complex supergene with the pigment loci, as is the case in the snail *Cepaea* (Cain *et al.*, 1968). Present evidence cannot distinguish among these or more complex models.

Another complication in the expression of pattern is developmental and could depend on environmental influences. Regardless of background color, the top (left) valve of a shell is always more heavily marked with pattern pigments than is the bottom (right) valve. Furthermore, “mottle & chevron”, the principal source of dark covering pattern, is most common on juveniles and on the juvenile portion of adult shells, indicating that the pattern is usually expressed on both valves early in life but then often ceases to be produced on the lower valve as the shell grows larger. A majority of adult shells show the “top valve only” pattern and often, but not always, these do have pigments in the juvenile region of the lower valve (Fig. 2e).

Other patterns are also expressed preferentially on one valve. The pattern “rays”, like “mottle & chevron”, is more common on top valves while the pattern “ribs only” is more common on bottom valves. There is very little evidence on the genetic status of these differences in pattern. Results from one mating suggest that the presence of the “mottle & chevron” pattern on both valves or on the “top valve only” is an allelic difference (Adamkewicz and Castagna, 1988). However, whether one gene controls the production of “episodic” pigments while another gene controls their distribution in various “covering” patterns or whether one complex locus with many variants controls both aspects of patterning is completely unknown.

The possible causes of these associations between valve, age, and pattern have never been investigated, but the contrast between valves and the shift in the expression of “mottle & chevron” do correspond to a shift in habitat that juveniles experience. During the first months of life, juvenile scallops cling to submerged objects, and both their valves are exposed to light and to the view of predators. After two or three months, the scallops drop onto the substratum and lie on their bottom (right) valves with only the top valves exposed. The overall lighter coloration of the lower valve may well be a response to this change of position. The patterns cannot, however, be entirely the product of environmental influences. Some scallops have both valves darkly pigmented throughout their lives, some show the “top valve only” pattern only on the adult portion of the shell, and some display the “top valve only” pattern throughout life, yet all experience the same shift in habitat. One possible explanation is that the change of habitat triggers a general lessening of pigmentation in the lower valve but that the mechanism by which the lightening is accomplished, and its extent, depends on the individual's particular genotype for a set of polymorphic pigment and pattern loci. Such interactions of genotype, age, and environment require that comparisons of pattern frequencies between age groups be made with great caution.

Table 6. Associations between pairs of pattern colors on top valves of adults were investigated with a series of 2 x 2 contingency chi squares for the presence/absence of each possible pair of colors in each pond. The number given for each pair is the Phi value (X^2/N), which measures the degree of association. The direction of associaton is shown by use of + and – symbols while the level of significance of the association is shown by the number + or – symbols. One, two, or three uses of the symbol indicates significance at the 0.05, 0.01, or 0.001 level respectively while ns indicated that the p value of the chi square was not significant. Data for Nashaquitsa Pond are in the upper right quadrant and data for Lagoon Pond are in the lower left.

	Slate	Brown	Chestnut	White	Gray	Yellow
Slate		+ + 0.11	ns	+ + + 0.47	+ + + 0.45	ns
Brown	+ 0.08		– – – 0.69	ns	+ + + 0.28	+ + + 0.51
Chestnut	ns	– – – 0.70		+ + + 0.16	– – – 0.20	– – – 0.64
White	+ + + 0.16	+ + + 0.16	+ + + 0.30		+ + + 0.19	– – – 0.29
Gray	+ + + 0.62	+ + + 0.18	– – – 0.15	+ + + 0.13		ns
Yellow	ns	+ + + 0.28	– – – 0.44	– – – 0.16	+ 0.08	

Table 7. Mean dimensions in millimeters of juvenile and adult shells from Lagoon and Nashaquitsa Ponds with standard deviations shown in parentheses. Shells from Lagoon Pond were significantly larger in all linear dimensions than shells from Nashaquitsa, the ANOVA for each comparison having $p < 0.01$. Although not tested for significance, relative depth (= depth/height) is also given.

		Height	Width	Depth	Rel. Depth	N
LAGOON POND:						
Juvenile	mean mm	18.2	18.4	7.4	0.404	231
	std error	± 0.34	± 0.39	± 0.16		
Adult	mean mm	52.50	55.40	23.10	0.440	302
	std error	± 0.30	± 0.33	± 0.16		
NASHAQUITSA POND:						
Juvenile	mean mm	15.9	15.7	6.0	0.377	377
	std error	± 0.13	± 0.15	± 0.06		
Adult	mean mm	48.20	50.70	22.10	0.456	310
	std error	± 0.35	± 0.37	± 0.20		

Regardless of how the various shell characters are produced, the significant difference in their frequencies for the same age groups in different ponds indicates that the two populations are relatively isolated from each other. The degree of genetic isolation of the two pond populations was not investigated directly in this study, but observations on the movement of scallop larvae out of the Niantic Estuary (Marshall, 1960; Moore and Marshall, 1967) give some indication of the isolation to be expected. These findings, like the present ones, suggest that there should be very little movement of larvae between ponds on Martha's Vineyard, particularly since the ponds open onto different bodies of water.

Differences between ponds could be a result only of their isolation, i.e. due only to genetic drift, or a result of selection based on differences in the environments of the two ponds. The ponds do differ in some physical parameters. Nashaquitsa Pond is smaller in area, shallower, and takes longer in the spring to reach the critical spawning temperature of 20°C than does Lagoon Pond (Elek, 1985). The salinities and substrata of the areas sampled were similar in both ponds as were plant and algal species on the substratum, while other aspects of the biological environment were not investigated. The earlier warming of Lagoon Pond probably explains the larger size attained by Lagoon scallops. The warmth not only increases the growth rate but also initiates earlier spawning, which provides a longer period for growth. As expected, if this is an important difference between the ponds, most of the total difference in mean size between the two populations was already achieved by the juvenile scallops.

The wide variety of colors and patterns is clearly a polymorphism of long standing. Both Abbott (1974) and Clarke (1965) have noted the existence of colors and patterns other than wild-type in *Argopecten*. Although Clarke did not make the distinction between background and pattern that the present authors do, his demonstration that the frequency of white bottom valves (the pattern "top valve only" of this paper) varies geographically proves that the polymorphism for pattern is widespread and of long standing. Furthermore, his remark that only white shells occurred in frequencies high enough to record suggests that the polymorphism is widespread and of long standing, with yellow and orange variants always rare. Additional evidence that the polymorphism for background color is neither new nor transient comes from a private collection of shells taken from Lagoon Pond in 1980. This sample was scored as containing 0.97 white, 0.013 yellow, and 0.017 orange shells. These counts are very similar to those in Table 2 and suggest that the polymorphism for background color is a persistent genetic polymorphism, at least on Martha's Vineyard. If this stability can be confirmed, drift will be a very unlikely explanation for the observed differences between ponds.

The highly significant difference in the frequency of yellow between adults and juveniles of Lagoon Pond provides some evidence that selection is acting on the polymorphism, but its meaning is not clear. Without data from several breeding seasons, one cannot know whether the difference is a unique event due to chance or a regular, biologically significant, occurrence indicating differential survival between colors. In light of the evidence that the polymorphism is neither new nor transient, any systematic selection against yellow at one stage would have to be balanced by an advantage in another area.

Those polymorphisms in marine mollusks that are, at least in part, understood appear to be driven by response to high temperatures. Mitton (1977) found a convincing relationship between temperature and the blue/brown polymorphism in the mussel *Mytilus edulis*, with the brown morph surviving high temperatures better and being more common in the southern part of the species range. Etter (1988) has found a similar relationship in the snail *Nucella lapillus* where white individuals survive better than brown ones in sheltered sites where the principal stress is temperature. It seems unlikely that temperature as a selective agent could account for differences between these two ponds, but its role should be carefully investigated both geographically and as one element of possible balancing selection.

Regardless of the pond in which they occur, the frequencies of the alleles for yellow and orange are low. Because both yellow and orange alleles are dominant, their combined frequency is estimated to be approximately 0.025 $(1 - \sqrt{0.95})$ and, if the population is near Hardy-Weinberg equilibrium, virtually all yellow and orange individuals should be heterozygous. The low frequencies of yellow and orange are interesting because they are examples of a polymorphism with rare dominants, and there has been considerable debate in the literature over mechanisms whereby rare dominants can be maintained in a population. Although the frequencies of yellow and orange are low, they are still too high for a balance between recurring mutation and selection to be the likely mechanism. Using the equation $H = 2v/s$ to estimate selection (Falconer, 1981), selection would have to be negligible ($s < 0.001$) unless the mutation was very high.

Another plausible mechanism, frequency-dependent or apostatic selection by visual predators giving an advantage to any rare morph, has been proposed by Clarke (1962). Moment (1962) has put forward a related theory of reflexive selection, proposing that the enormous number and variety of colors in some natural populations may be an adaptation in itself, providing protection against predation by visually discriminating predators such as fish and birds. Moment (1962) cites the enormous range of variation in *Donax* species as one example of reflexive selection, and *Argopecten irradians irradians*, with its wide range of colors and patterns may be another example of reflexive selection. Frequency dependent selection, as described by Clarke and Moment, could account for the persistence of rare dominants in the stable polymorphism in the population of scallops on Martha's Vineyard.

The documented molluscan, echinoderm and crustacean predators of scallops are unlikely to be the agents sustaining the polymorphism because they are primarily non-visual predators. However, vertebrate predators such as teleost fish and birds could provide selection pressures based on shell color, especially in juveniles with their brighter, unfouled colors and exposed habitat. Although there is no documentation, fish are probably important predators on juvenile scallops and could be responsible for the observed differences between age groups and ponds. Birds have been reported as taking quite large scallops. Gutsell (in Broom, 1976) reported that Herring Gulls, *Larus argentatus* Pontoppidan, catch many scallops at low tide, and diving ducks have also been reported taking large numbers of shellfish. Kortright (1967) recorded twelve species of diving ducks (sub-family: Nyrocinae) for which mollusks comprise up to 80% of their diet. Of these, he cited the White-Winged Scoter, *Melanitta fusca deglandi* (Linnaeus), and the American Scoter, *M. nigra* (Linnaeus), as major predators, with scallops forming about half the total food of both species of scoters. Today large numbers of diving ducks overwinter in the vicinity of Martha's Vineyard and are major predators of shellfish in the region. Thus, it seems very possible that shore birds are providing the frequency-dependent selection necessary to sustain the polymorphism of shell color in the populations of scallops which have been described in this paper.

Argopecten irradians has all of the elements necessary to make it a promising subject for ecological and evolutionary genetic studies. The species has an extensive polymorphism with a genetic basis and with rare dominants, its populations are known to differ in the frequencies of the morphs, and an extensive suite of visual predators is known. In addition, the species probably shows variation in its polymorphism on a geographical scale. An elucidation of the forces acting on this system would permit comparison with the polymorphisms in other marine mollusks and an evaluation of the roles of environmental stresses such as temperature, of predation, and of random events in maintaining natural variation.

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PREHISTORIC FRESHWATER MUSSEL (NAIAD) ASSEMBLAGES FROM SOUTHWESTERN IOWA

JAMES L. THELER
DEPARTMENT OF SOCIOLOGY AND ANTHROPOLOGY
UNIVERSITY OF WISCONSIN, LA CROSSE
LA CROSSE, WISCONSIN 54601, U.S.A.

ABSTRACT

Archaeological excavations at nine prehistoric Indian sites along the Missouri River drainage of southwestern Iowa produced 275 freshwater mussel (naiad) valves representing at least 13 species. These subfossils are the remains of mollusks collected as a food resource and to obtain shells for use as tools. While little historic data are available for this region, distribution records show that all 13 mussel taxa were widespread historically in the south central Missouri River drainage. The archaeological data indicate that molluscan communities having a similar species composition to those in the region today have been present for a millennium or more.

There is no published information on the distribution of freshwater mussel (Mollusca: Bivalvia: Unionidae) species in the streams and rivers of southwestern Iowa. It can be assumed from historic distributional data that the streams of this area once supported a mussel fauna similar to that of adjacent regions. The freshwater mussel valves recovered from prehistoric Indian sites in southwestern Iowa provide an opportunity to evaluate the distribution of naiad mollusks of this region prior to EuroAmerican settlement.

Mussel valves from nine archaeological sites in southwestern Iowa are considered in this report. The oldest mussel assemblage is from the Hanging Valley Site (13HR28), which overlooks the Little Sioux River near its confluence with the Missouri River in Harrison County, Iowa (Fig. 1). Hanging Valley is a Woodland Tradition cemetery and habitation site used at about A.D. 400 (Tiffany *et al.*, 1988). The remaining eight archaeological sites are Glenwood Culture earthlodges, occupied between approximately A.D. 1000 and A.D. 1300 (Hotopp, 1978). The Glenwood earthlodges are located in Mills County, Iowa; seven of these were situated along the Pony and Keg creeks which form a small tributary to the Missouri River. The other earthlodge (13ML176) was located immediately adjacent to the Missouri River valley a few miles north of the Pony and Keg creeks cluster (Fig. 1).

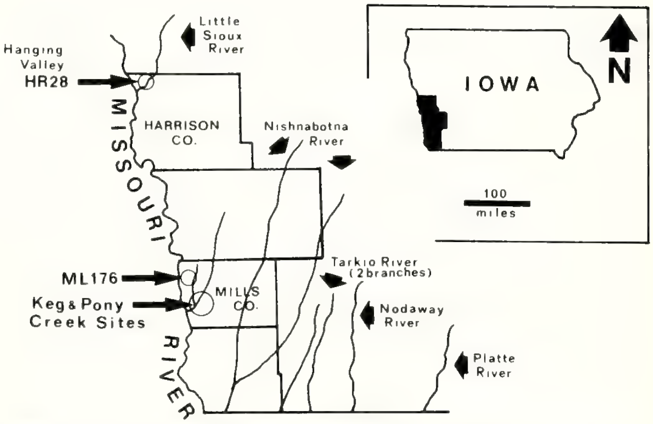

Fig. 1. Location of archaeological sites in southwestern Iowa from which freshwater mussel valves were obtained.

METHODS AND MATERIALS

The southwestern Iowa subfossil mussel valves were identified by the author at the University of Wisconsin, La Crosse, and now are housed permanently in the Archaeological Repository at the Office of the State Archaeologist, University of Iowa, Iowa City, Iowa. Naiad taxonomy used in this report follows the nomenclature presented by Turgeon *et al.* (1988). Table 1 provides a listing of the number of valves of each taxon for each archaeological site. A comparison of the subfossil naiades with historic naiad faunas recorded from the Missouri River and its tributary streams in northwestern and west central Iowa, northwest Missouri and portions of North and South Dakota are presented in Table 2.

RESULTS

In all, 275 valves of 13 mussel species are represented

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Table 1. Distribution and number of freshwater mussel valves recovered from prehistoric archaeological sites in southwestern Iowa.

Drainage:	Little Sioux R.	Missouri River	Keg Creek					Pony Creek			
Site Number:	13HR28	ML176	ML128	ML130	ML131	ML132	ML135	ML126	ML136	Total Valves	% of Total
Family Unionidae											
Subfamily Anodontinae											
Anodonta grandis	—	1	—	—	—	—	1	—	—	2	0.7
Lasmigona complanata complanata	—	6	—	—	1	2	1	—	3	13	4.7
Subfamily Ambleminae											
Tritogonia verrucosa	2	2	—	2	—	—	1	1	3	11	4.0
Quadrula quadrula	—	4	—	2	—	—	1	1	—	8	2.9
Q. pustulosa pustulosa	—	1	—	—	—	—	—	—	—	1	0.4
Amblema plicata plicata	—	45	3	1	4	8	8	7	10	86	31.3
Fusconaia flava	—	6	—	—	—	3	1	3	1	14	5.1
Subfamily Lampsilinae											
Leptodea fragilis	2	—	—	—	1	—	—	—	—	3	1.1
Potamilus alatus	18	1	—	—	3	1	1	1	5	30	10.9
Ligumia recta	—	4	—	—	1	2	3	—	4	14	5.1
Lampsilis teres	1	3	—	—	—	—	—	—	—	4	1.5
L. siliquoidea	—	4	—	—	—	—	3	—	—	7	2.5
L. cardium	1	22	—	2	12	14	21	1	6	79	28.7
L. sp.	—	—	—	—	—	—	—	1	2	3	1.1
Totals	24	99	3	7	22	30	41	15	34	275	100.0

at the nine southwestern Iowa archaeological sites (Table 1). The two most abundant species were *Amblema plicata plicata* (Say, 1817), with 86 valves equalling 31.3% of the combined site specimens, and *Lampsilis cardium* (Rafinesque, 1820), with 79 valves (28.7%); shells of both taxa occurred at eight of the nine states. *Potamilus alatus* (Say, 1817) recovered at seven sites was next in abundance with 30 valves representing 10.9% of all naiad valves. *Fusconaia flava* (Rafinesque, 1820) and *Ligumia recta* (Lamarck, 1819), both having a total of 14 valves each (5.1%), were recovered at five of the nine sites and rank fourth in abundance. The remaining eight taxa, in decreasing frequency of occurrence, are given in Table 1.

DISCUSSION

Utterback (1915) presented the distribution of mussel taxa found in three small northwest Missouri rivers that flow from southwestern Iowa. These include, from east to west, the Platte, Nodoway and Tarkio rivers, but unfortunately, the Nishnabotna River, flowing almost entirely through southwestern Iowa, was not considered. All of the above streams drain into the Missouri River. The distribution of freshwater mussels in the Missouri River along the Nebraska border with Iowa was presented by Hoke (1983). In west central Iowa, data on the modern distribution of mussels in the middle and upper portions of the Little Sioux River were presented by Rausch and Bovbjerg (1973). The naiad fauna of other Missouri tributaries including the Big Sioux, James and Vermillion rivers in northwest Iowa, and the Dakotas was reported by Coker and Southall (1914) (Figs. 1, 2).

A comparison of the southwestern Iowa subfossil mussel assemblage composition with survey data for streams in the adjacent parts of the Missouri River basin shows that all 13 subfossil taxa were recorded historically in the region. Eleven species, *Anodonta grandis, Lasmigona complanata complanata, Tritogonia verrucosa, Quadrula quadrula, Q. pustulosa pustulosa, Amblema plicata plicata, Fusconaia flava, Leptodea fragilis, Potamilus alatus, Ligumia recta* and *Lampsilis teres* are recorded for northwestern Missouri streams draining southwestern Iowa, while two species represented in the archaeological assemblage, *Lampsilis siliquoidea* and *L. cardium*, are not recorded historically from the Missouri River adjacent to Iowa (Hoke, 1983) or from northwestern Missouri streams (Utterback, 1915-16; Oesch, 1984). However, both *L. cardium* and *L. siliquoidea* have been recorded in historic times in the Missouri River drainage north of southwestern Iowa (Table 2).

Although valves representing many mussel taxa recovered at the southwestern Iowa archaeological sites exhibited signs of human modification by grinding and/or flaking to produce tools, the large cup-like valves of *Lampsilis cardium* seem to have been especially favored by prehistoric peoples who easily converted these shells into a variety of spoons and cups. It is probable that *L. cardium* valves were intentionally sought by aboriginal peoples for utensil production. This taxon's widespread occurrence and the presence of numbers of unmodified valves seems to argue for local populations in suitable southwestern Iowa habitat prior to

EuroAmerican settlement.

Six naiad taxa having a limited historic distribution in the Missouri River drainage are absent from the southwestern Iowa archaeological record; these include *Anodonta suborbiculata* Say, 1831, *Strophitus undulatus* (Say, 1817), *Alasmidonta marginata* Say, 1818, *Arcidens confragosus* (Say, 1829), *Obliquaria reflexa* Rafinesque, 1820 and *Truncilla donaciformis* (Lea, 1828). *Potamilus ohiensis* (Rafinesque, 1820), while widespread historically in this portion of the Missouri River basin (Table 2), also is not present in the southwest Iowa subfossil assemblage. *Potamilus ohiensis* is at the northwestern margin of its range in the Missouri River drainage and has perhaps occupied (or at least become widespread in) this region only in the historic period. *Pleurobema coccineum* (Conrad, 1834) is recorded during historic times in at least three streams feeding the Missouri River, but has not been recorded as a southwestern Iowa subfossil.

Freshwater mussel valves also have been reported in prehistoric context at the Woodland Tradition Rainbow site (13PM91) in Plymouth County, Iowa (Riggle and Freitag, 1981). This northwestern Iowa site is located adjacent to the Floyd River, a tributary to the Missouri River. The Rainbow site naiad

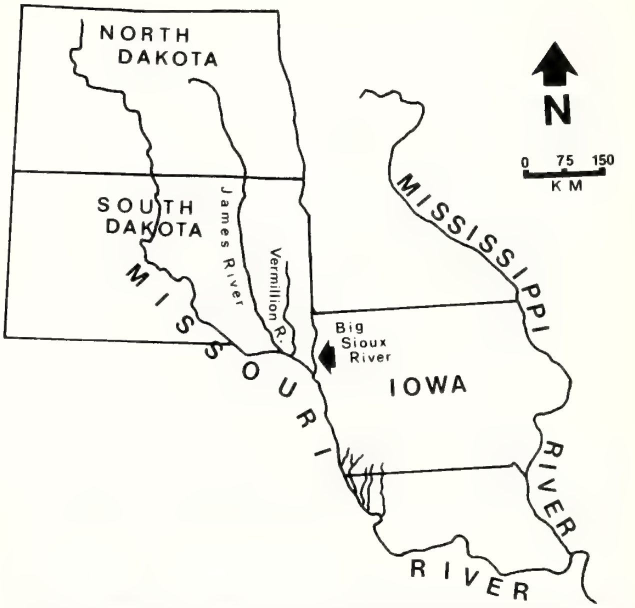

Fig. 2. Location of selected streams with documented freshwater mussel populations in the south central Missouri River drainage.

Table 2. A comparison of naiad shells from archaeological sites in southwestern Iowa with historic naiad distribution in portions of the Missouri River drainage (P, taxon present; —, taxon absent) (1, Hoke, 1983; 2, Utterback, 1915-16; 3, Rausch and Bovbjerg, 1973; 4, Coker and Southall, 1914).

Data Source:	This Report Subfossils (n=275 valves)	Missouri R.[1] Adjacent to Iowa	Tarkio R.	NW Missouri[2] Nodaway R.	Platte R.	Little Sioux R.[3]	Big Sioux R.[4]	James R.[4]	Vermillion R.[4]
Family Unionidae									
Subfamily Anodontinae									
Anodonta suborbiculata	—	P	—	—	—	—	—	—	—
A. grandis	0.7	P	P	—	P	P	—	P	P
Strophitus undulatus	—	—	—	—	P	—	—	—	—
Alasmidonta marginata	—	—	—	—	—	—	P	—	—
Arcidens confragosus	—	—	—	—	—	—	—	P	—
Lasmigona complanata complanata	4.7	P	P	P	P	P	P	P	P
Subfamily Ambleminae									
Tritogonia verrucosa	4.0	—	P	P	P	—	—	P	—
Quadrula quadrula	2.9	—	P	P	P	P	—	P	P
Q. pustulosa pustulosa	0.4	—	P	P	P	—	P	P	P
Amblema plicata plicata	31.3	—	P	P	P	P	P	P	P
Fusconaia flava	5.1	—	—	—	P	—	—	—	—
Pleurobema coccineum	—	—	—	—	—	—	P	P	P
Subfamily Lampsilinae									
Obliquaria reflexa	—	—	—	—	P	—	—	—	—
Truncilla donaciformis	—	—	—	—	P	—	—	—	—
Leptodea fragilis	1.1	P	P	P	P	P	P	P	P
Potamilus alatus	10.9	—	P	P	P	—	P	P	P
P. ohiensis	—	P	P	P	P	P	—	—	—
Ligumia recta	5.1	—	—	—	P	P	P	P	P
Lampsilis teres	1.5	—	P	—	P	—	—	P	—
L. siliquoidea	2.5	—	—	—	—	—	P	P	P
L. cardium	28.7	—	—	—	—	P	P	P	P
L. sp.	1.1	—	—	—	—	—	—	—	—

assemblage contains 11 of the 13 taxa recorded as subfossils in southwestern Iowa, lacking only *Tritogonia verrucosa* and *Quadrula quadrula*. Three species, *Lasmigona costata* (Rafinesque, 1820), *L. compressa* (Lea, 1829) and *Actinonaias ligamentina* (Lamarck, 1819) not recovered in the southwestern Iowa subfossil assemblages or recorded in this region during the historic period, are reported as members of the Rainbow site subfossil assemblage. All three of the above taxa are on their range margin in the Missouri River drainage of northwestern Iowa, judging from historic distributions (Clarke, 1985; La Rocque, 1967). Like the southwestern Iowa archaeological assemblages, the Rainbow subfossil material did not contain *Anodonta suborbiculata* or *Potamilus ohiensis*.

The distribution of common and rare mussel taxa found in southwestern Iowa is paralleled in other aboriginal assemblages when compared to adjacent modern stream faunas. Klippel *et al.* (1978) reported 25 species of freshwater mussel from the modern Pomme de Terre River of western Missouri, while archaeological deposits at nearby Rodgers Shelter contained only 16 species. The authors indicate that 10 of the 11 species absent from Rodgers Shelter are small size or low frequency taxa that could have failed to have been collected by aboriginal mussel harvestors. Thin shelled taxa, missing from the assemblage, may not have been preserved Klippel *et al.* (1978).

The Mississippi River in the vicinity of Prairie du Chien, Wisconsin, once contained approximately 44 mussel species (Havlik and Stansbery, 1978). Extensive aboriginal shell deposits at Prairie du Chien were found to contain 28 mussel species (Theler, 1987). As is the case in southwestern Iowa, reported here, and western Missouri (Klippel *et al.*, 1978), those species absent from archaeological deposits are, for the most part, taxa that are of small size or are those found to be rare in historic times (Theler, 1987). As with all archaeological assemblages mussels, those of southwestern Iowa have passed through a "filter" of human cultural behavior and must be evaluated in that light.

CONCLUSIONS

The assemblages of subfossil mussel valves recovered from nine archaeological sites in southwestern Iowa contained 13 of 21 taxa recorded during the historic period for the south central portion of the Missouri River and its tributaries considered in this report. The 13 species represented as archaeological subfossils were found to be widespread in the region historically. Generally, those naiad taxa that were rare in historic surveys were species not represented among the southwest Iowa archaeological assemblages. One exception is *Potamilus ohiensis,* found to be widespread in the region during the historic period, but absent from the subfossil assemblages. It is possible that *P. ohiensis* could have extended its range or increased in abundance in the Missouri River basin since EuroAmerican settlement of the region.

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RESEARCH NOTE

RECTIFICATION OF THE NOMENCLATURE OF CERTAIN SPECIES OF TRICULINE SNAILS TRANSMITTING *PARAGONIMUS* AND *SCHISTOSOMA* IN CHINA

LIU YUE YING
INSTITUTE OF ZOOLOGY
ACADEMIA SINICA
BEIJING, CHINA

GEORGE M. DAVIS
ACADEMY OF NATURAL SCIENCES
OF PHILADELPHIA
PHILADELPHIA, PENNSYLVANIA 19103, U.S.A.

To date, 12 species that transmit *Paragonimus* or *Schistosoma* in China have been classified as *Tricula* Benson, 1843 (Liu, *et al.,* 1980, 1983a, b, 1984; Liu, 1983 and unpub. data). *Tricula* has been considered by Chinese workers to belong to the family Hydrobiidae (Liu *et al.* 1980, 1983a, b; Kang, 1983, 1984; Liu, 1983). However, intensive studies of *Tricula* and allied genera have shown that the family Hydrobiidae does not occur in China or Southeast Asia; *Tricula* belongs to the Pomatiopsidae; Triculinae: Triculini (Davis, 1979, 1980; Davis *et al.* 1983, 1984, 1986a, b).

Recent collaboration between the Institute of Zoology and the Academy of Natural Sciences has enabled us to reexamine all Triculinae species names associated with the transmission of human disease. This was necessary because early identifications were based on the original descriptions of Gredler (1885-1892), Heude (1890) and Annandale (1924a, b) and the photographs of Gredler's types by Yen (1939). All of these sources were truly inadequate in detail of description, size of printed photographs, and illustrations showing intrapopulation variation and accordingly misidentifications were inevitable. One of us (Davis) has recently studied and photographed the type specimens and it is now possible to reevaluate the identifications of specimens in China associated with disease transmission. Annandale's types are in the British Museum; Gredler's paralectotypes are in the Senckenberg Museum, Frankfurt am Main, Germany; Heude's *Tricula* types are in the Museum of Comparative Zoology at Harvard University and the Academy of Natural Sciences of Philadelphia.

A complicating factor is that species currently assigned to *Tricula* in China actually belong to at least two genera: *Tricula* Benson, 1843 and *Neotricula* Davis 1986. Generic distinction is based on detailed comparative anatomy; one cannot separate the genera on shell or radular characters. The generic distinctions are illustrated in figure 1. The description of *Tricula* is based on the comparative anatomy of northern India *T. montana* Benson, 1843; the type species is from northern India (Davis *et al.*, 1986b). The description of *Neotricula* is based on *Lithoglyphopsis aperta* Temcharoen 1971 [a species later relegated to *Tricula* (Davis, 1979) from the Mekong River of Thailand and Laos].

Neotricula: 1) The oviduct runs from gonad to the pallial oviduct without making a twist or coil; 2) the duct of the seminal receptacle arises from the duct of the bursa (or spermathecal duct); 3) the spermathecal duct runs to the end of the mantle cavity beside the pericardium; it does not enter the pericardium; 4) a slender sperm duct connects the duct of the bursa to the oviduct; 5) the wall of the pericardium is a thin unspecialized membrane; 6) The pericardium does not bulge out into the mantle cavity.

Tricula: 1) The oviduct makes a tight coil or twist dorsal to the bursa copulatrix; 2) the duct of the seminal receptacle arises from the oviduct; 3) the spermathecal duct runs to, and enters the pericardium; 4) there is no sperm duct; the duct of the bursa joins the oviduct; 5) the wall of the pericardium is considerably thickened and specialized to accommodate sperm; 6) the pericardium bulges out into the mantle cavity.

A second complicating factor is that there are numerous species of *Tricula sensu lato* (*Tricula* as understood prior to Davis *et al.,* 1986b) spread throughout southern China. There are at least 20 valid species known today. There are

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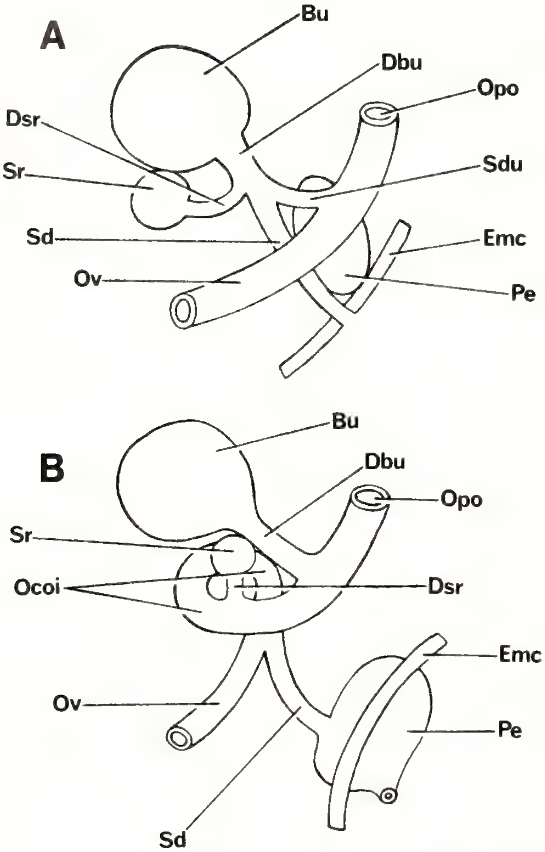

Fig. 1. Bursa copulatrix complex of organs showing differences between *Neotricula* (A) and *Tricula* (B) [Bu, bursa copulatrix; Dbu, duct of the bursa; Dsr, duct of the seminal receptacle; Emc, posterior end of the mantle cavity; Ocoi, oviduct coil; Opo, opening of pallial oviduct into the albumen gland (posterior pallial oviduct); Ov, oviduct; Pe, pericardium; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle).

many undescribed species; the number of newly described species increases each year and will continue to do so for some time. We estimate that there are more than 60 such species throughout China (see Kang, 1983, 1984a, b, 1986; Liu *et al.*, 1983a, b, 1987; Guo and Gu, 1985; Davis, *et al.*, 1986a).

A third complicating factor is that confirmation that a species transmits a parasite is dependent on voucher specimens cataloged into museum or institutional collections. The voucher specimen system has not been used in China except for type specimens; we encourage its use. The number assigned to the specimens should be referenced in the publication linking a parasite to the snail population in question. This assures future investigators that the specimens seen in a collection are the ones specified in the publication. A poor illustration of a single specimen in a publication does not serve to identify the species.

Given the above difficulties, we comment on eight taxa currently listed in the literature as transmitting parasites for which nomenclatural changes are necessary or where there is substantial confusion. We have anatomical data for only three of these, i.e. *Neotricula jinhongensis, Tricula gregoriana*, and *T. montana*. All others must be retained in *T. sensu lato* until anatomical data are available.

1. *Tricula guangxiensis* Liu *et al.*, 1983a. This is a synonym of *T. fuchsi* (Gredler 1887). *T. fuchsi* transmits *Paragonimus skrjabini.*

2. *Tricula minutoides* (Gredler, 1885): Specimens from Hunan [Institute of Zoology, Academia Sinica, (IZAS) catalog number 00643] are actually *T. cristella* Gredler 1887. *T. cristella* transmits *Paragonimus skrjabini.*

3. *Tricula cristella* (Gredler, 1887): (IZAS No. 00615): These specimens are not that species; they belong to an apparently undescribed species. Genuine *T. cristella* does not transmit *Paragonimus hueitungensis.*

4. *Tricula gregoriana* Annandale, 1924a: There is much confusion in the literature concerning this species. Specimens figured by Liu *et al.* (1984) (IZAS No. 00642) are not that species but *Delavaya dianchiensis* Davis and Guo, 1986 (in Davis *et al.*, 1986a). Illustrations published by Sun (1959) as *T. gregoriana* are also not that species. Davis *et al.* (1986a) published a description of the anatomy of snails from Yunnan referable to *T. gregoriana* by comparison with the types. There specimens are deposited in the collections of the Institute of Zoology, Beijing with IZAS No. 08701 - (F).

5. *Tricula humida* Heude, 1890: There is much confusion concerning the identity of this species. It is possible that specimens illustrated by Sun (1959) are this species, but it is not possible to confirm the identification from the reduced photographs. We have not seen any specimens in various collections in China that compare favorably with the type series. Accordingly, we cannot confirm that *T. humida* transmits *Paragonimus.*

6. *Tricula jinhongensis* Guo and Gu, 1985: This is a species of *Neotricula*; it transmits *Paragonimus skrjabini* and *Schistosoma* sp. The parasite has not been identified to species.

7. *Tricula montana* Benson, 1843. Contrary to Liu *et al.*, 1983a, this species does not occur in China. It is restricted to the lesser Himalayan mountains of northern India west of Nepal. On the basis of comparative anatomy the closest association with *Tricula* in China is with *T. gregoriana.*

8. *Halewisia sinica* Liu *et al.*, 1983b: The genus *Halewisia* is confined to the lower Mekong River in Thailand, Laos and Cambodia. *H. sinica* from China is possibly *Tricula sensu lato* but generic confirmation will depend on anatomical data. *T. sinica* transmits *Paragonimus skrjabini.*

In conclusion, it is clear that considerable confusion would be avoided if specimens found to transmit parasites were formally cataloged into a permanent institutional collection with samples also deposited in various national centers. The catalog numbers should be published with the data. Descriptions of species and assignment to genera demands detailed comparative anatomical data; it is no longer acceptable to describe species of Triculinae on the standards of Stimpson (1865): shell, radula, operculum, penis. Characters of these structures are too convergent to use for these purposes.

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SYMPOSIUM ON THE BIOLOGY OF THE SCAPHOPODA

ORGANIZED BY
RONALD L. SHIMEK
PARAMETRIX, INC.

AMERICAN MALACOLOGICAL UNION
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FUNCTIONAL MORPHOLOGY OF THE PERIANAL SINUS AND PERICARDIUM OF *DENTALIUM RECTIUS* (MOLLUSCA: SCAPHOPODA) WITH A REINTERPRETATION OF THE SCAPHOPOD HEART

PATRICK D. REYNOLDS
BIOLOGY DEPARTMENT, UNIVERSITY OF VICTORIA,
VICTORIA, BRITISH COLUMBIA, V8W 2Y2, CANADA

ABSTRACT

The anatomy and ultrastructure of the perianal blood sinus and pericardium in the scaphopod *Dentalium rectius* Carpenter were investigated. The perianal blood sinus surrounds the rectum and lies adjacent to the anterior wall of the pericardial coelom; the sinus is enclosed by smooth musculature with additional muscular trabeculae traversing the sinus. The pericardium is contractile and consists of a simple, flat epithelium with interspersed muscle fibres; both are separated from the haemocoel by a basal lamina. The pericardial musculature is arranged as laterally oriented trabeculae which produce localized transverse constrictions of the dorsal pericardial wall. There is no evidence for a heart enclosed by the dorsal wall of the pericardial coelom in a position ventral to the stomach as interpreted by earlier workers, as both a myocardium and distinct epicardium are absent. A portion of the pericardial epithelium apposing the perianal sinus musculature is developed into podocytes and could be the site of primary urine production. Although organogenetic information on scaphopod coelom formation is lacking, structural similarities of the perianal sinus and pericardium in *D. rectius* to the heart and pericardium in other molluscan classes support the homology of these organs.

The morphology of scaphopod circulatory structures received a great deal of attention up to the early part of this century, producing several conflicting interpretations of structure and function. Deshayes' (1825) and Clark's (1849) descriptions of a heart in *Dentalium* spp. appear to be mistaken identifications of the esophagus and stomach, respectively. Lacaze-Duthiers (1857) found no structure analogous to a molluscan heart in *Dentalium* sp., i.e. a pulsatile vessel within a pericardium responsible for the movement of blood, and he considered the contractions of the pedal, perianal and abdominal blood sinuses to be sufficient for circulation. A small serous sac within the anterior abdominal sinus, and lying between the stomach and ventral body wall, was suggested by Lacaze-Duthiers (1857) as the pericardial rudiment; he also noted the structural similarities of the perianal sinus to the bivalve ventricle. Fol (1889), studying *D. entalis* (Deshayes), concluded that the perianal sinus is homologous with the heart of other molluscs.

Plate (1891, 1892) described a completely different structure as representing the scaphopod heart; an invagination of the dorsal pericardial wall, lying ventral to the stomach and within the pericardial coelom. Boissevain (1904) and Distaso (1905) confirmed these results and agreed with this interpretation. While Potts (1967) states that the pericardium is absent in scaphopods and the heart is represented by a contractile vessel, most recent reviews accept Plate's findings, at least tentatively (Fischer-Piette and Franc, 1968; Martin, 1983; Andrews, 1988).

Defining the structure of the scaphopod heart and pericardium accurately and conclusively is of importance not only in ascertaining the level of organization of the circulatory system, but also in determining the role of the heart in excretion or, alternatively, the structural modification of the excretory system in the absence of a functional heart in this molluscan class. The general organization of the excretory system in the Mollusca is based on a haemocoel-pericardium-kidney complex. Physiological work on prosobranchs (Harrison, 1962; Little, 1965), coleoid cephalopods (Harrison and Martin, 1965; Martin and Aldrich, 1970) and bivalves (Jones and Peggs, 1983; Hevert, 1984) has established that primary urine is produced by ultrafiltration into the pericardial coelom. The site of ultrafiltration, as characterized ultrastructurally by the presence of podocytes, varies from the auricular or ventricular wall in prosobranch gastropods (Andrews, 1981), polyplacophorans (Økland, 1980), protobranch and pteriomorph bivalves (Pirie and George, 1979; Meyhöfer *et al.*, 1985), to the branchial heart wall in cephalopods (Witmer and Martin, 1973; Schipp and Hevert, 1981) and the antero-dorsal wall of the pericardium in heterodont bivalves (Meyhöfer *et al.*, 1985). In all cases, the ultrafiltrate enters the pericardial

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cavity from the haemocoel and passes through a renopericardial connection to the kidney lumen. Further modification of the primary urine by reabsorption and secretion takes place before excretion to the external environment via the mantle cavity.

Localization of an ultrafiltration barrier by ammoniacal carmine injection, a technique used extensively in the study of circulation and excretion up to the early 1900's, has been attempted in representatives of most molluscan classes and has served as a useful basis for subsequent morphological and quantitative physiological investigation in many representative species (for a review, see Martin, 1983). In scaphopods, however, it is the only physiological method applied to date, and possible sites of ultrafiltration have not been clearly indicated. Working with *Dentalium* sp., Kowalevsky (1889) noted the accumulation of ammoniacal carmine in unspecified blood spaces and connective tissue cells. Using the same method with *D. vulgare* Da Costa, Cuénot (1899) found that these cells contain yellowish, oily granules and broadly described their distribution as similar to that in amphineurans and gastropods, being found under the epithelium, between the viscera and within the interstices of muscle fibres. On the basis of an uncertain, but presumed common excretory function, Cuénot (1899) aligned these ammoniacal carmine accumulating cells and those of amphineurans and gastropods with the pericardial glands of bivalves and branchial hearts of cephalopods. Strohl (1924) agreed, labelling the cells collectively as carmine athrocytes.

An internal opening between the paired kidneys and another coelomic (pericardial) space is absent in *Dentalium* sp. according to Lacaze-Duthiers (1857), Fol (1885, 1889) and Plate (1888, 1892). Of those investigations which describe a pericardium, only Distaso (1905) noted a morphological connection represented by a pore leading to the left kidney.

The present study of *Dentalium rectius* Carpenter (Order Dentaliida) aims to clarify the morphological relationship between the perianal and abdominal haemal sinuses, the pericardial coelom and the kidney using light and electron microscopy. The tissues of the pericardium and associated blood sinuses are described ultrastructurally with particular reference to contractile elements, and with a view to identifying possible sites for ultrafiltration of blood. The information contributes toward a better understanding of circulation and excretion in the Scaphopoda, and relationships of the class within the Mollusca.

MATERIALS AND METHODS

Specimens of *Dentalium rectius* were dredged from approximately 60 m at Satellite Channel, close to Victoria, British Columbia, Canada. For anatomical examination at the light microscope level, tissues were fixed in 10% seawater--buffered formalin, dehydrated in a graded ethanol series and embedded in paraffin. Serial sections of 6-8 μm thickness were stained with eriochrome cyanin (Chapman, 1977). Additionally, serial 1 μm sections of resin embedded material, prepared as described below for transmission electron microscopy (TEM), were stained with methylene blue-azure II.

Tissues for electron microscopical examination were dissected from specimens and fixed in 2.5% glutaraldehyde in 0.2M phosphate buffer (pH 7.4) and 0.14M NaCl for 2 hours at room temperature. After rinsing in 0.2M phosphate buffer and 0.3M NaCl, they were post-fixed using 1% osmium tetroxide in 0.1M phosphate buffer and 0.375M NaCl for one hour at 4°C. Tissues were rinsed in distilled water and dehydrated in a graded series of ethanol. Specimens for scanning electron microscopy (SEM) were critical point dried from CO_2, sputter coated with gold and examined in a JEOL JSM-35. Specimens for TEM were transferred to propylene oxide before embedding in epon resin. Ultrathin sections (grey-silver-pale gold interference colour) were obtained on a Reichert ultramicrotome and stained with uranyl acetate and lead citrate (Reynolds, 1963) prior to viewing in a Philips EM-300 transmission electron microscope.

Observations of live animals were made using a Wild M5A dissecting microscope. Removal of the shell and a ventral dissection of the mantle wall revealed the anus and transparent ventral body wall through which the pericardium could be seen easily.

RESULTS

PERIANAL SINUS

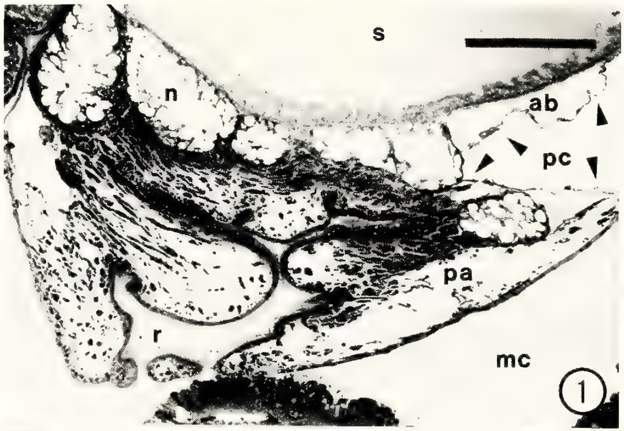
The perianal sinus surrounds the rectum as it passes between the kidneys to the mantle cavity. The sinus is positioned antero-ventrally to the kidneys and the pericardium, and no other coelomic space surrounds or apposes it (Fig. 1). The sinus is surrounded by circular and longitudinal musculature, is traversed by an array of muscle fibres or trabeculae, and has additional longitudinal and circular fibres along the inner wall of the sinus enveloping the rectum (Fig. 2).

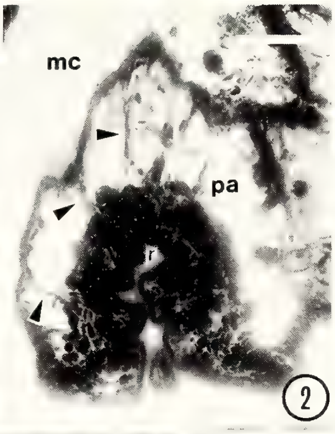
The musculature of the perianal sinus is smooth. Neural processes occur adjacent to muscle cells, although no synapses have been observed (Fig. 3). The muscle cells contain thick (29-58 nm diameter) and thin (5.8 nm diameter) myofilaments which are interspersed with α-glycogen granules (17.4 nm). Similar granules are also found concentrated at the periphery of the cell adjacent to the 6-11 nm wide sarcolemma (Fig. 4). Thick myofilaments have an axial periodicity of 9-15 nm (Fig. 5). Mitochondria are located in clusters within sarcoplasmic bulges adjacent to contractile elements (Fig. 4).

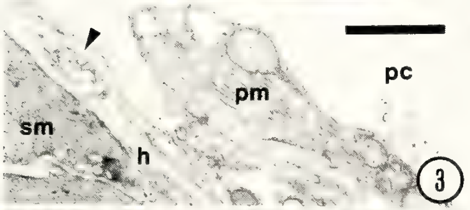
The muscular walls of the perianal sinus repeatedly contract, causing an extension of the rectum and closing of the anus, followed by relaxation of the rectum and dilation of the anus, occurring at a rate of approximately 40-60 contractions per minute. Occasional periods of relaxed dilation last from 10 to 30 seconds. These contractions, in addition to propelling blood through the sinus, appear to facilitate the voiding of strings of faecal material from the rectum.

PERICARDIUM AND DORSAL PERICARDIAL FOLDS

The pericardial coelom lies within the abdominal blood







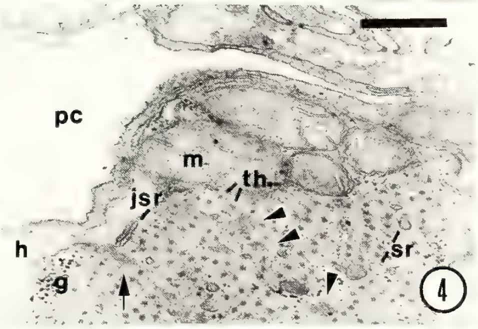


Fig. 1. Longitudinal section through the perianal sinus (pa), kidney (n), and anterior portion of stomach (s) and pericardium (arrowheads) (ab, abdominal sinus; mc, mantle cavity; pc, pericardial cavity; r, rectum). Scale bar = 0.1 mm. **Fig. 2.** Oblique cross section of the perianal sinus (pa), showing traversing muscular trabeculae (arrowheads) (mc, mantle cavity; r, rectum). Scale bar = 40 μm. **Fig. 3.** Muscle cells of the perianal sinus (sm) and the pericardium (pm). Note neural process adjacent to perianal sinus musculature (arrowhead) (h, haemocoel; pc, pericardial cavity; pe, pericardial epithelial cell). Scale bar = 1 μm. **Fig. 4.** Cytoplasmic extensions of a pericardial epithelial cell overlying a muscle cell of the perianal sinus (arrowheads, dense bodies; arrow, attachment plaque; g, glycogen granules; h, haemocoel; jsr, junctional sarcoplasmic reticulum; m, mitochondrion; pc, pericardial cavity; sr, sarcoplasmic reticulum; th, thick myofilaments). Scale bar = 0.5 μm. **Fig. 5.** Thick myofilaments of the smooth perianal sinus muscle cell. Note axial periodicity within the filaments. Scale bar = 0.2 μm.

sinus, ventral to the stomach, and extends from the posterior end of the stomach to the kidneys and perianal sinus, to which it adheres anteriorly (Figs. 1, 6-8). The ventral pericardial epithelium is always in close contact with the body wall, while irregular infoldings of the dorsal pericardial wall project into the coelomic cavity. There is no myocardium or any type of endothelium within these foldings (Figs. 1, 7, 8); the only musculature adjacent to the pericardium is that of the body wall ventrally and perianal sinus anteriorly (Figs. 6, 7). A connection exists between the pericardial coelom and the right kidney (Fig. 9), although it was not found in all specimens.

The pericardial wall is composed of three cell types: simple flat epithelium, interspersed with muscle cells, and modified in the region adjacent to the perianal sinus to include podocytes. The arrangement and ultrastructure of epithelial and muscle cells is similar throughout the pericardium (Fig. 6). The epithelial cells (Fig. 10) typically possess a cell body with a small amount of cytoplasmic material surrounding the nucleus. The cell bodies extend into the pericardial cavity, with the continuous basal lamina lining the haemocoel. Thin cytoplasmic branches extend between cell bodies and contain one or a few isolated mitochondria in addition to α- (15 nm) and β- (37 nm) glycogen granules (Figs. 10-12). Desmosomes, with an intercellular distance of 9-15 nm, occur frequently where epithelial cell junctions appose the basal lamina (Fig. 11) but were not observed in areas where cytoplasmic extensions overlap adjoining muscle cells (Fig. 12). Adjoining plasmalemmae are not highly infolded and do not interdigitate (Fig. 12).

The pericardial musculature is arranged as trabeculae which run in an entirely transverse direction, and are discontinuous in both anterior-posterior and lateral axes of the pericardium. The width of the trabeculae varies between 1 and 10 μm (Figs. 13, 14). Muscle cells are interspersed between the epithelial cells and typically underlie extensions of the epithelial cytoplasm (Figs. 12, 15-18). Adjoining plasmalemmae of the two cell types have an intercellular space of 7-15 nm within which no extracellular material has been observed (Figs. 12, 15, 16, 18). Desmosomes occur at cell junctions apposing either the basal lamina or coelomic space, and have an intercellular width of 9-15 nm (Fig. 16, 18). Both cell types are separated from the haemocoel by a continuous basal lamina, 18-40 nm thick (Figs. 12, 15-18). A thin layer of collagen fibrils, varying in thickness from 0.11-0.53 μm, is often associated with the basal lamina (Fig. 15). Neural elements are found adjacent to the muscle cells (Fig. 17).

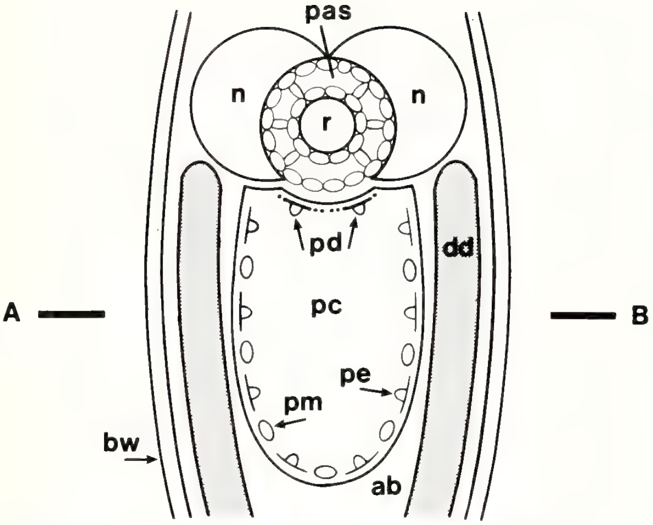


Fig. 6. Schematic diagram showing the relative positions of the perianal sinus (pas), pericardium (pc) and kidneys (n) (ab, abdominal sinus; bw, body wall; dd, digestive diverticulum; pd, podocytes; pe, epithelial cell of the pericardium; pm, muscle cell of the pericardium; r, rectum; A-B indicates cross-sectional view represented in figure 7).

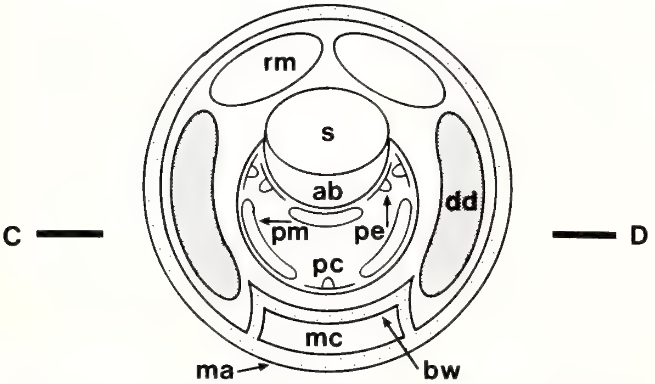


Fig. 7. Schematic diagram showing the relative positions of the stomach (s), pericardium (pc) and mantle cavity (mc) (ab, abdominal sinus; bw, body wall; dd, digestive diverticulum; ma, mantle; pe, epithelial cell of the pericardium; pm, muscle cell of the pericardium; rm, retractor muscle; C-D indicates frontal section view represented in figure 6) (See also figure 17).

Muscle fibres of the pericardium fixed in a contracted state show near-alignment of dense bodies (0.12-0.14 μm length, 46-58 nm width) into Z-lines, with the intervening thick myofilaments creating A and I lines in a loose sarcomeral structure, approximately 1 μm in length (Fig. 19). Occasional attachment plaques were observed anchoring the filaments to the sarcolemma (Fig. 19). The muscle cells have a diameter at the nucleus of 3-3.5 μm (Fig. 20). Thick and thin myofilaments do not appear to have a regular arrangement with respect to each other, and have diameters of 18-33 nm and 6-7.5 nm respectively (Figs. 16, 18). Profiles of rough and smooth sarcoplasmic reticulum are present as are those of junctional sarcoplasmic reticulum (Figs. 16, 18, 19). A small quantity of α- and β- glycogen granules is present within the cytoplasm of the cell periphery (Fig. 16). Clusters of mitochondria are positioned between the contractile elements and sarcolemma; sarcolemmal width is 7-15 nm (Fig. 21).

The pericardium contracts independently of the perianal sinus in a regular though discontinuous manner; there is neither a gradual peristalsis of the pericardium nor a simultaneous uniform contraction of all muscle fibres. The contractions occur in an anterior to posterior progression of 2-3 discrete constrictions of the dorsal pericardial wall, the wholly transverse orientation of the muscle fibres producing a single localized transverse constriction which is released as another, posterior to this, is produced. The posterior end of the pericardium appears to lie free within the abdominal sinus and moves in an anterior-posterior direction due to contraction of the muscle fibres. The anterior wall remains in close contact with the kidneys and perianal sinus, as the ventral pericardial wall does with the body wall. Very infrequently a slight contraction of the stomach was observed.

The third cell type of the pericardium is the podocyte, which is characterized by the presence of pedicels and fenestrations in the cytoplasmic branches of the pericardial epithelium (Figs. 22-26). The cell type is not widespread and has only been observed in areas apposed by smooth musculature in the region of the perianal sinus, i.e. the anteroventral portion of the pericardium (Figs. 6, 23, 24). Fenestrations, 13-32 nm in width, are distributed along cytoplasmic extensions (Figs. 22-26), and raised pedicels have also been observed (Fig. 25). In some sections, diaphragms in the form of electron opaque strands bridge the fenestration (Fig. 26). In all cases, the fenestrations overlie the basal lamina; there is no evidence of an apposing collagen layer. No microvilli line the luminal surface of these or any cells of the pericardium.

DISCUSSION

STRUCTURE OF THE MOLLUSCAN HEART

The anatomy of the molluscan heart generally consists of a single ventricle and one or two auricles which usually correspond to the number of ctenidia. The whole is enclosed within a pericardium, and the ventricle in the Bivalvia and some Gastropoda is traversed by the rectum (Jones, 1983). At the height of molluscan heart organization, the Cephalopoda possess a complex systemic heart associated with a closed circulatory system (Wells, 1983); at the other extreme, the Scaphopoda have been described as having a rudimentary heart, relying on body musculature for circulation through a series of sinuses (Hill and Welsh, 1966). The molluscan heart lies freely within the pericardium, although the pericardial cavity does not extend dorsally over the ventricle in the Neomeniomorpha (Salvini-Plawen, 1985) and the bivalve *Pteria* (White, 1942). In some bivalve species the dorsal wall of the ventricle remains attached to the pericardium by connective tissue (Narain, 1976). The presence of the pericardium is critical to circulatory function; the pressure of the pericardial fluid is normally less than that of the blood

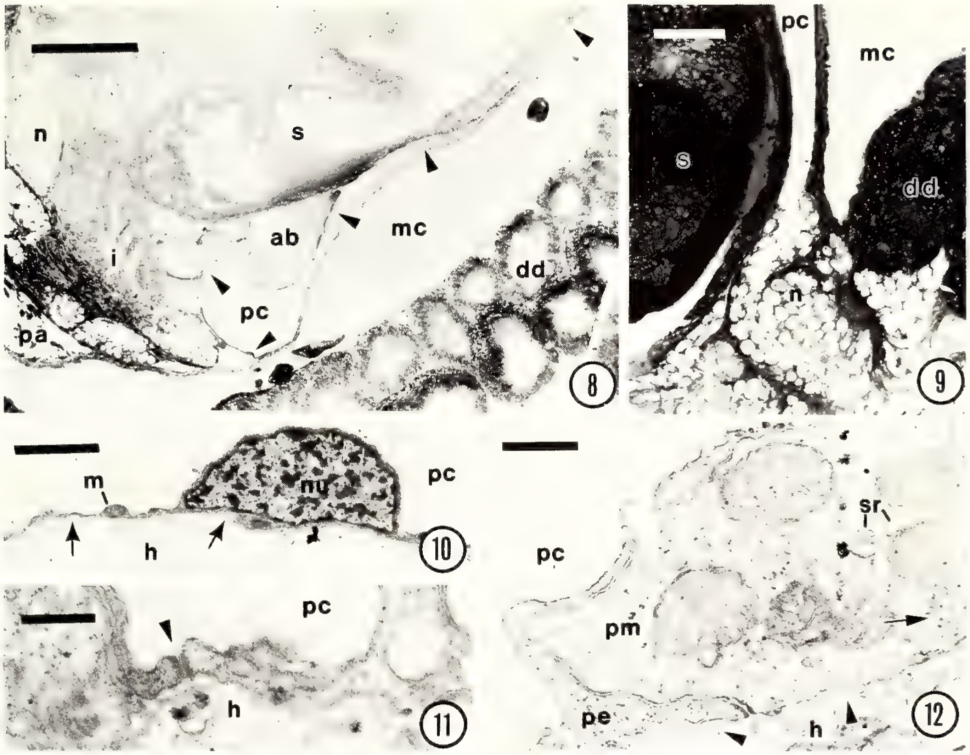


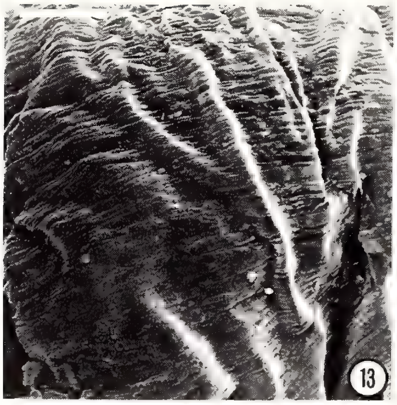
Fig. 8. Longitudinal section through the pericardium (pc), stomach (s), perianal sinus (pa) and kidney (n) (arrowheads, anterior and dorsal pericardial walls; ab, abdominal sinus; dd, digestive diverticulum; i, intestine; mc, mantle cavity). Scale bar = 0.15 mm. **Fig. 9.** Longitudinal section showing connection between the pericardial cavity (pc) and the right kidney (n) (dd, digestive diverticulum; mc, mantle cavity; s, stomach). Scale bar = 50 μm. **Fig. 10.** Pericardial epithelial cell (arrow, basal lamina; h, haemocoel; m, mitochondrion; n, kidney; pc, pericardial cavity). Scale bar = 2.5 μm. **Fig. 11.** Cytoplasmic extensions of the pericardial epithelium (arrowhead, desmosome; h, haemocoel; pc, pericardial cavity). Scale bar = 0.3 μm. **Fig. 12.** Epithelial (pe) and muscle cells (pm) of the pericardium (arrowhead, basal lamina; arrow, myofilaments; h, haemocoel; pc, pericardial cavity; sr, sarcoplasmic reticulum). Scale bar = 0.6 μm.

in the heart, and cardiac refilling is maintained by a volume-compensating mechanism as originally proposed by Ramsay (1952) and Krijgsman and Divaris (1955), and reviewed by Jones (1983). The pericardium is drained by one or two renopericardial canals, which connect the lumina of the pericardium with those of the kidneys (Martin, 1983).

At the cellular level, the molluscan heart consists of an epicardium, which rests on a basal lamina, and an inner loose myocardium; an endothelium is lacking (Narain, 1976; Økland, 1980; Jones, 1983) except in cephalopods, where it is incomplete (Jensen and Tjønneland, 1977). While in some cases the epicardial cells possess microvilli and can also have a secretory role (Kling and Schipp, 1987), the ventricular epicardium generally consists of a continuous, simple epithelium. Podocytes are usually concentrated within the auricular epicardium, and are characterized by the presence of numerous thin cytoplasmic extensions termed pedicels, which are aligned in a parallel array over the continuous basal lamina, between the haemocoel and coelomic spaces (Andrews, 1976; Pirie and George, 1979; Økland, 1980). The gaps between the pedicels create fenestrations in the epithelium or ultrafiltration slits; the basal lamina separates the haemocoel from pericardial coelom, and acts as the functional filter (Andrews, 1981; Morse, 1987). In many bivalves, gastropods and cephalopods the ultrafiltration slits are bridged by slit diaphragms (Boer and Sminia, 1976; Andrews, 1979; Schipp and Hevert, 1981; Meyhöfer *et al.,* 1985), although these have not been found in the podocytes of chitons (Økland, 1980). Portions of the auricular epicardium or pericardial epithelium are elaborated in many species, particularly in bivalves, to form pericardial glands (White, 1942), within which extensive areas of podocytes have been found (Meyhöfer *et al.,* 1985). A similar development of the haemocoel-pericardial interface is seen in the branchial heart appendages of coleoids and the pericardial appendages of nautiloid cephalopods (Fiedler and Schipp, 1987). The molluscan pericardium consists primarily of simple epithelial cells, although there have been few detailed ultrastructural studies. The polyplacophoran pericardial epithelium is continuous with, while differing from, the ventricular and auricular epicardium (Økland, 1980); it also possesses muscle cells and is pulsatile (Greenberg, 1962; Økland, 1981).

INTERPRETATIONS OF SCAPHOPOD CIRCULATORY STRUCTURES TO DATE

Two structures have been proposed as representing the scaphopod heart: (i) the perianal sinus, which has been described as having morphological similarities to (Lacaze-



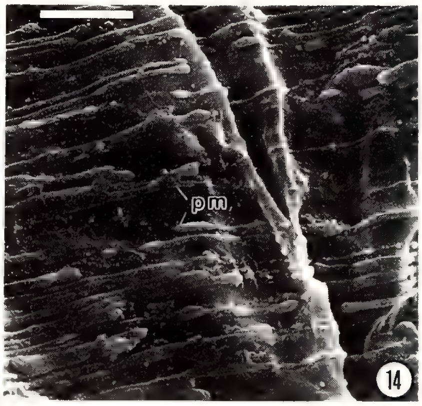
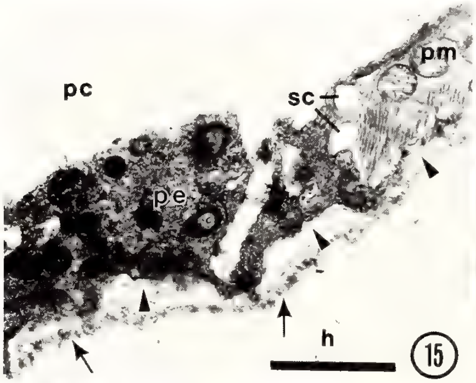
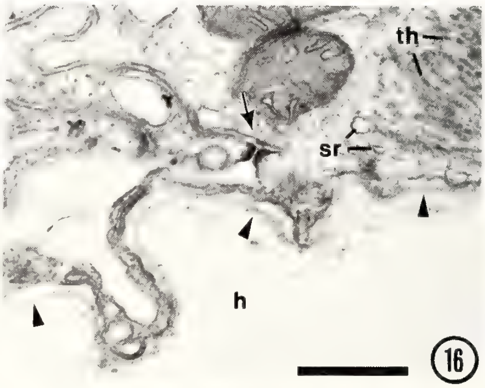
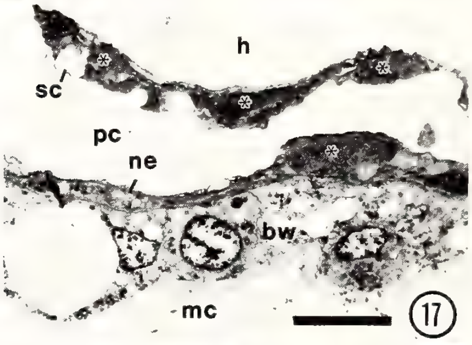
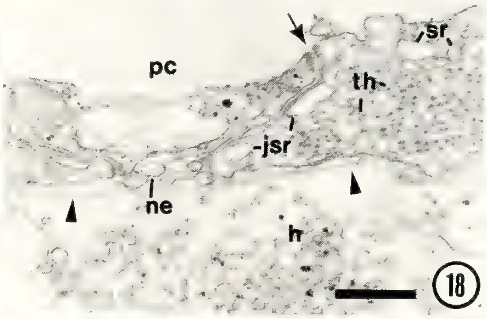


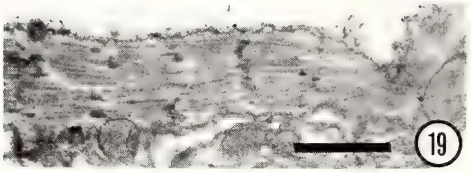
Fig. 13. Dorsal pericardial wall, viewed from the pericardial cavity. Anterior is to the top of the photomicrograph. Note lateral orientation of muscle fibres. Scale bar=0.15 mm. **Fig. 14.** Dorsal pericardial wall, viewed from the pericardial cavity. Anterior is to the top of the photomicrograph. Note the discontinuity of the pericardial muscle cells (pm) along anterior-posterior and lateral axes. Scale bar = 40 μm.











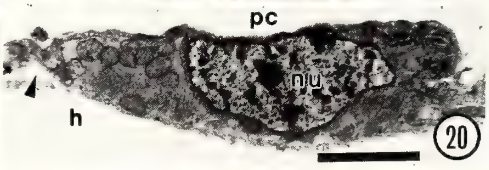


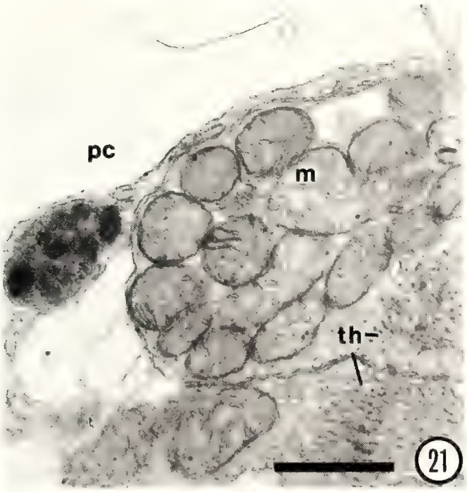
Fig. 15. Epithelial (pe) and muscle cells (pm) of the pericardium (arrowhead, basal lamina; arrow, collagen fibres; h, haemocoel; pc, pericardial cavity; sc, subsarcolemmal cisternae). Scale bar = 2 μm. **Fig. 16.** Junction of epithelial (pe) and muscle cells (pm) of the pericardium (arrowheads, basal lamina; arrow, desmosome; h, haemocoel; sr, sarcoplasmic reticulum; th, thick myofilaments). Scale bar = 0.5 μm. **Fig. 17.** Longitudinal section of dorsal (top) and ventral (bottom) pericardial walls and body wall (bw) (*, muscle cells of the pericardium; h, haemocoel; mc, mantle cavity; ne, nerve process; pc, pericardial cavity; sc, subsarcolemmal cisternae). Scale bar = 10 μm. **Fig. 18.** Junction of epithelial and muscle cells of the pericardium (arrowheads, basal lamina; arrow, desmosome; h, haemocoel; jsr, junctional sarcoplasmic reticulum; ne, nerve process; pc, pericardial cavity; sr, sarcoplasmic reticulum; th, thick myofilaments). Scale bar = 0.7 μm. **Fig. 19.** Longitudinal section through pericardial muscle cell. Note loose sacromeral structure formed by alignment of dense bodies. Scale bar = 0.15 μm. **Fig. 20.** Oblique cross section through pericardial muscle cell (arrowhead, basal lamina; h, haemocoel; nu, nucleus; pc, pericardial cavity). Scale bar = 3 μm.

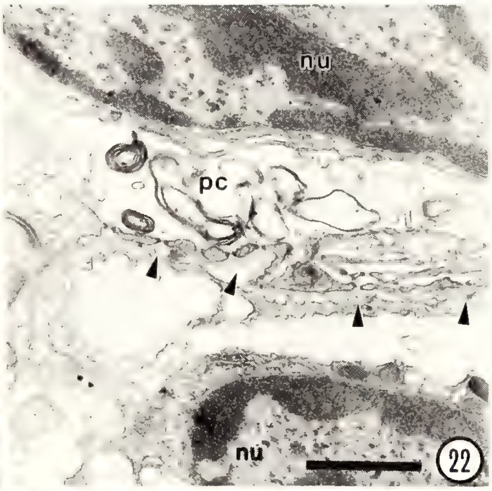
Duthiers, 1857) and homology with (Fol, 1889) the bivalve ventricle; and (ii) the dorsal infolding of the pericardium, ventral to the stomach, described by Plate (1891, 1892), Boissevain (1904), and Distaso (1905). Lacaze-Duthiers (1857) did not discuss the relationship between the perianal sinus and molluscan heart in any detail. Fol (1889), however, based their homology on structural similarities, describing the position of the sinus in relation to the rectum, the musculature and rhythmic contractions of the sinus, and an endothelium which Plate (1892) and Boissevain (1904) later refuted. Lacaze-Duthiers (1857) placed the major responsibility for movement of the blood with the large pedal sinus, while Fol (1889) agreed that the perianal sinus makes little contribution to circulation.

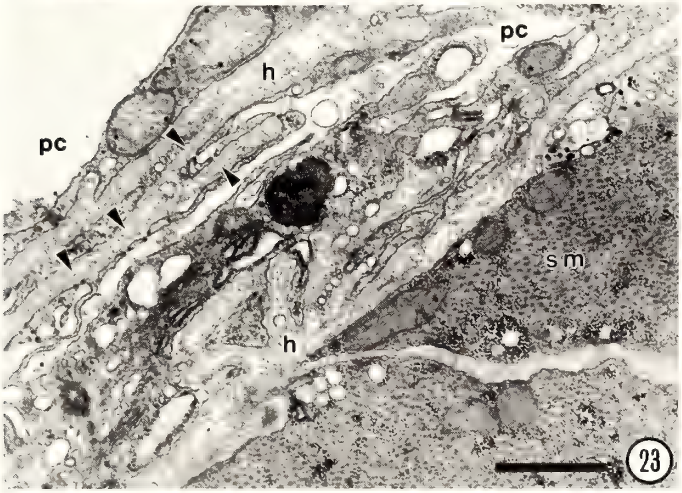
The studies by Plate (1891, 1892), which were confirmed by Boissevain (1904) and Distaso (1905), described a contractile vessel ventral to the stomach, surrounded by the pericardial coelom. Plate (1892) stated that the heart is extraordinarily simple, with no chambers or vessels, and lacks a strong development of musculature. He found that the pericardial and heart walls did not differ histologically, and were composed of epithelial cells with very thin, parallel and regularly arranged fibres. While Plate (1892) suggested that these could be muscle fibres, he concluded that this structure could not act as a center of propulsion for the circulatory system.

CIRCULATORY STRUCTURES IN *DENTALIUM RECTIUS*

In *Dentalium rectius*, there is no evidence of the ultrastructural features associated with the typical molluscan heart (i.e. a myocardium with an associated epicardium) in a position ventral to the stomach and enclosed by the peri-







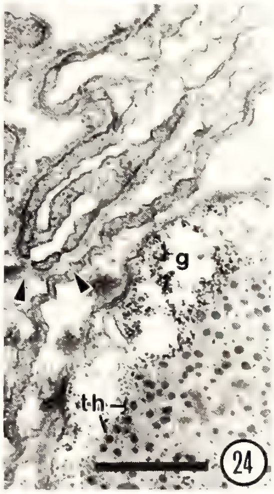


Fig. 21. Junction of pericardial muscle cells (m, mitochondrion; pc, pericardial cavity; th, thick myofilaments). Scale bar = 1 μm. **Fig. 22.** Podocytes in the pericardium. Note fenestrations in the pericardial epithelium apposed by basal lamina (arrowheads) (nu, nucleus; pc, pericardial cavity). Scale bar = 1 μm. **Fig. 23.** View of perianal sinus muscle cells (sm) and pericardium. Note the highly infolded cytoplasmic extensions of the pericardium overlying the perianal sinus musculature, and the fenestrations apposed by basal lamina (arrowheads) (h, haemocoel; pc, pericardial cavity). Scale bar = 1 μm. **Fig. 24.** Muscle cell of perianal sinus (sm) and fenestrations (arrowheads) in the overlying pericardium (g, glycogen granules; th, thick myofilaments). Scale bar = 0.7 μm.

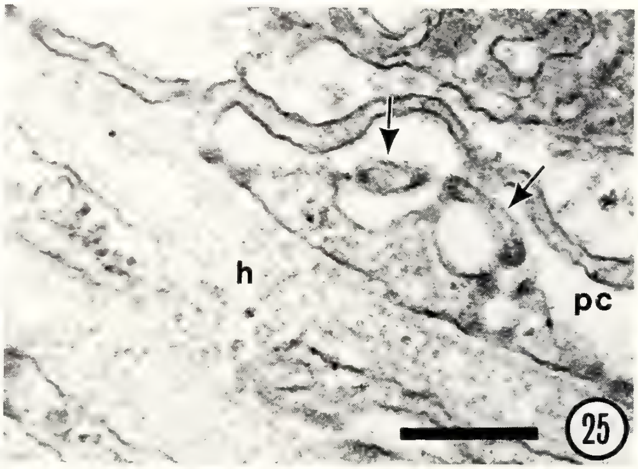
cardium as described by Plate (1891, 1892), Boissevain (1904) and Distaso (1905) for other species of *Dentalium*. Without the benefit of ultrastructural study, it is likely that these early investigators considered the contractile dorsal pericardial wall as a ventricular epicardium. The lack of a myocardium or any ultrastructural differentiation of this portion of the pericardial epithelium discounts this interpretation, and no evidence supporting homology with the molluscan ventricle exists. While the scaphopod stomach is described as possessing a muscular tunic (Salvini-Plawen, 1988), the musculature in *D. rectius* is discontinuous and closely applied to the stomach wall and as such is not associated with the pericardium and does not enclose a portion of the haemocoel.

The homology of the pericardial coelom described by Lacaze-Duthiers (1857), Plate (1891, 1892), Boissevain (1904) and Distaso (1905) with that of other molluscs is based solely on its general anatomy, i.e. a closed sac composed of squamous epithelium within the haemocoel. Ultrastructural features of the pericardial epithelium in *Dentalium rectius* support this homology; the presence of long cytoplasmic branches, desmosomes and few other organelles suggest a simple delimiting epithelium, similar to that found in other molluscan peri- and epicardia. Furthermore, an excretory role inferred from the presence of podocytes and a renopericardial connection also supports this homology. On this basis the term *pericardium* should be retained in describing this structure in scaphopods.

The arrangement of musculature in the *Dentalium rectius* pericardium suggests transverse contractions of the dorsal pericardial wall, which are supported by the observations of live animals. The contractile pericardia in the Polyplacophora have been suggested by Økland (1981) to function in the circulation of pericardial fluid as part of the excretory system, with little effect on the contraction mechanisms of the heart. In *Tonicella*, the epithelial and muscle cells are separated by collagen and basal lamina, which is, however, continuous with the basal lamina lining the epithelial cells (Økland, 1981). In comparison, no extracellular material exists between cell types in the pericardium of *D. rectius*, and the basal lamina is limited to an unbranching layer between the pericardial elements and haemocoel. Contractions of the dorsal pericardial wall in *D. rectius* undoubtedly contribute to the circulation of blood through the relatively large abdominal sinus. These contractions do not lead directly to ultrafiltration of blood through the dorsal pericardial wall due to the absence of podocytes in this area of the pericardium. However, it is possible that local increases in blood pressure could be transferred anteriorly to the perianal sinus and ultimately facilitate ultrafiltration via the podocytes lining the perianal sinus. The irregular invaginations of the dorsal pericardial wall of *D. rectius* seen in section and considered by Plate (1891, 1892), Boissevain (1904) and Distaso (1905) in other *Dentalium* species to be the heart, are due to the state of contraction of the dorsal pericardial wall at fixation and do not represent a permanently enclosed contractile vessel. The ventral pericardial wall was always observed in close adherence to the body wall in both fixed and live material.

The presence of podocytes is a development of the pericardial epithelium that is commonly observed and interpreted in other molluscan classes as the site of ultrafiltration of blood and production of primary urine. While ultrastructural features such as apposition of basal lamina, fenestration width and the presence of slit diaphragms in the podocytes of *Dentalium rectius* are consistent with such a function, there is no evidence of an extensive array of pedicels and ultrafiltration slits as seen in representatives of some other molluscan classes (Andrews, 1979; Meyhöfer *et al.*, 1985). Thus, the area available for ultrafiltration appears to be quite limited in *D. rectius*.

The renopericardial connection with the right kidney is small (20 μm in diameter), and was only noted in incidental thin (1 μm) sections. A left renopericardial canal in *Dentalium* was described by Distaso (1905), although it appears from reading his account that the dorso-ventral orientation of the animal is opposite to that generally accepted by other investigators of the Scaphopoda. Therefore, considering the mantle cavity as ventral and the larger aperture as



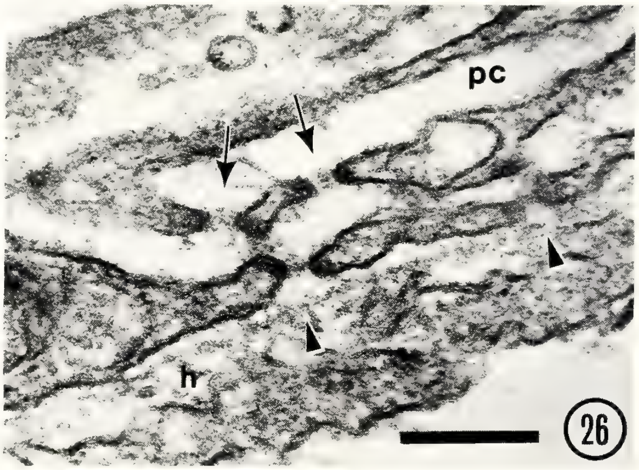


Fig. 25. Podocytes of the pericardium. Note raised pedicels (arrows) (h, haemocoel; pc, pericardial cavity). Scale bar = 0.3 μm. **Fig. 26.** Podocytes of the pericardium. Note fenestrations in epithelium apposed by basal lamina (arrowheads) and bridged by diaphragms (arrows) (h, haemocoel; pc, pericardial cavity). Scale bar = 0.3 μm.

anterior, Distaso (1905) had, in fact, also described a connection between the pericardium and right kidney.

The ultrastructure of the perianal sinus in *Dentalium rectius* does not differ significantly from that of smooth molluscan cardiac muscle. Thick myofilaments have an axial periodicity resembling paramyosin, while myofibre size, the arrangement of glycogen and mitochondria, and the development of the sarcoplasmic reticulum is similar to that found in the cardiac musculature of the bivalves *Venus* (Kelly and Hayes, 1969), *Elliptio* (Rutherford, 1972) and *Geukensia* (Watts *et al.,* 1981), and of the polyplacophorans *Lepidopleurus* and *Tonicella* (Økland, 1980). This is in contrast with the obliquely striated heart musculature of gastropods and cephalopods, as reviewed by Kling and Schipp (1987). The position of the sinus in *D. rectius* in relation to the rectum parallels that found in the bivalve ventricle. Also, the presence of traversing muscular trabeculae, which produce the regular contractions of the sinus (this study; Fol, 1889; Plate, 1892; Fischer-Piette and Franc, 1968), is also found in the ventricles of many bivalves and gastropods (Narain, 1976; Økland, 1982; Jones, 1983).

Whether the perianal sinus, pericardium and kidneys in *Dentalium rectius* have an associated ontogenesis reflecting the developmental pattern of the heart, pericardium and kidneys from a common anlagen as seen in other classes of molluscs (Raven, 1966; Moor, 1983) with a subsequent movement of the pericardium from a position surrounding the ventricle to one more posterior to it, awaits further information on scaphopod organogenesis. If an homology between these organs exists, the lack of aortae, auricles or valves of any description, and the limited apposition of the pericardium, indicate a much reduced heart compared to that found in other molluscan classes. This reduction could have developed as a consequence of altered circulatory requirements, due in large part to the loss of ctenidia from the uniquely modified scaphopod mantle cavity.

Unidirectional flow of blood through the perianal sinus is not maintained (pers. obs.). While contractions could produce local pressures capable of driving limited ultrafiltration, it is unlikely to be capable of overcoming peripheral resistance of the circulatory system, or of even contributing significantly to circulation of the blood. As a consequence of the contractions of the foot and body musculature, however, the perianal sinus may serve a role in facilitating equilibration of pressure gradients between the pedal and abdominal blood sinuses.

In conclusion, there is no evidence for a heart within the pericardium of *Dentalium* as interpreted by Plate (1891, 1892), Boissevain (1904), and Distaso (1905). Ultrastructural features in *Dentalium rectius* suggest that there could be an homology of the perianal sinus and pericardium with the heart and pericardium of other molluscs. Studies of scaphopod organogensis are necessary to confirm this. The contractility of the dorsal pericardial wall and the perianal sinus may facilitate ultrafiltration of the blood via podocytes, which are limited to the anterior portion of the pericardium and overlie the perianal sinus. Further study into the blood pressures created by these and other contractile structures of the *Dentalium* haemocoel is necessary to further delineate their respective contributions to circulation.

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DIET AND HABITAT UTILIZATION IN A NORTHEASTERN PACIFIC OCEAN SCAPHOPOD ASSEMBLAGE

RONALD L. SHIMEK[1]
BAMFIELD MARINE STATION
BAMFIELD, BRITISH COLUMBIA
CANADA V0R 1B0

ABSTRACT

The diets of *Dentalium rectius* Carpenter, 1864, *Pulsellum salishorum* Marshall, 1980, and *Cadulus aberrans* Whiteaves, 1887 were determined by examination of buccal pouch contents of specimens collected and examined quarterly from December 1983 to December 1984. *D. rectius* was omnivorous, ingesting a wide variety of food items including sediment particles, fecal pellets, kinorhynchs, and various invertebrate eggs; however, foraminiferans were the most numerous prey. *D. rectius* was most abundant in a silty area containing about 10% organic material by weight; however, it was found in all areas sampled. *D. rectius* ranged in abundance from about 5 animals/m^2 in clean sand to about 66 animals/m^2 in silt. Foraminiferans were rare where *D. rectius* was most abundant.

Cadulus aberrans preyed preferentially upon the foraminiferans *Cribrononion lene* and *Rosalina columbiensis.* The robust foraminiferan *Elphidiella hannai* was readily accepted as prey, while the fragile *Florilus basispinatus* were taken less frequently than expected, as were *Buliminella* spp. *C. aberrans* was found most frequently in sandy substratum consisting of about 5% organic material by weight. Foraminiferans were common in this habitat. The average density of *C. aberrans* was about 10 animals/m^2.

Pulsellum salishorum was a dietary specialist preying on the foraminiferan *Cribrononion lene. P. salishorum* was relatively uncommon (6 animals/m^2) but evenly distributed in all habitats examined.

Due to selective predation on foraminiferans, scaphopods appear to alter relative abundances and size-frequency distributions of their prey populations. The numerical dominance of *Florilus basispinatus, Buliminella elegans,* and *Buliminella exilis* and the relative rarity of *Cribrononion lene* are probably direct results of scaphopod predation. Most of the prey items were less than 300 μm in diameter.

Dentalium rectius is able to thrive in areas of low populations of foraminiferans by utilizing alternative foods. Predation by *D. rectius* and *Pulsellum salishorum* in these habitats probably causes these low populations.

Scaphopods, uncommon members of most shallow-water marine ecosystems, have seldom been studied. The diets and some natural history attributes are known for a few species, usually based on small sample sizes or limited to short periods of observation (Davis, 1968; Gainey, 1972; McFadien, 1973; Bilyard, 1974; Poon, 1987). Generally, previous studies were made on members of the order Dentalioida, with few observations on species in the other scaphopod order, Gadilida (Davis, 1986; Carter, 1983; Poon, 1987).

Scaphopods are the only wholly infaunal molluscan class and are relatively abundant in deep-sea communities. They are also abundant in the unconsolidated sediments of the fjord systems north of the Strait of Juan de Fuca on the West Coast of North America (Shimek, 1988, 1989). In these areas, with the exception of minute bivalves such as *Axinopsida serricata* (Carpenter, 1864), scaphopods are often the dominant mollusks with several sympatric species.

Morton (1959) referred to the Scaphopoda as the "most uniform group" of mollusks. Scaphopods are generally considered to be predators upon foraminiferans (Lacaze-Duthiers, 1856, 1857; Morton, 1959; Dinamani, 1964; Fisher-Piette and Franc, 1968; Gainey, 1972; Bilyard, 1974; Taib, 1980; Carter, 1983; Poon, 1987). I examined several scaphopod communities in Barkley Sound on the southwest side of Vancouver Island, British Columbia to determine diet and habitat utilization in order to address the possibility of competition for either food or habitat.

I tested the hypothesis that these communities contained representatives of different species that were eating

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[1] Current address: 25022 144th Place S.E., Monroe, Washington 98272, U.S.A.

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similar prey and living in the same habitats. To examine this general hypothesis, I asked several specific questions about diet. Do these animals eat the same general category of prey? Within those categories, do these animals prey upon representatives of the same species? Are the prey similar in size or shape? Does the diet vary seasonally or with reproductive condition of the predator? Do the prey vary with the habitat or are scaphopods feeding on similar prey among various habitats? I asked similar questions about the habitats where the scaphopods were collected. What were the physical characteristics of the habitats? Could the distribution of either the scaphopods or their prey be correlated with any particular physical parameter of the habitat?

MATERIALS AND METHODS

Scaphopods for this study were collected at three sites in Barkley Sound (Table 1). The most abundant scaphopods were *Dentalium rectius* Carpenter, 1864, *Cadulus aberrans* Whiteaves, 1887, and *Pulsellum salishorum* Marshall, 1980. Other sympatric species were *C. californicus* Pilsbry and Sharp, 1898, *C. tolmiei* Dall, 1897, and *D. pretiosum* Sowerby, 1860. Some of the latter three species were more common in other habitats, but these were not included in this study.

Quantitative collections were made using a 0.1m^2 Petersen bottom grab. Two replicate samples were collected from each station in December, 1983 and March, June, September and December, 1984. After every haul, the grab was inspected to insure adequate substratum penetration and complete jaw closure. The grab was further examined to check for evidence of sample loss due to winnowing. If the grab functioned incorrectly, that sample was discarded and a replacement taken. Each sample was deposited in a sorting tray, and a 1 l subsample of substratum was retained for later particle size and composition analyses. The remaining sediment was washed gently through a 0.5 mm screen and all scaphopods were retained.

At each site a beam trawl or anchor dredge was used to collect additional scaphopods. Specimens to be examined alive were cleaned of any adherent sediment, placed in clean sea water, and returned to Bamfield Marine Station. During transport and handling, the animals were maintained below 15°C. Exposure to higher temperatures is generally lethal to scaphopods (Shimek, 1988). At the laboratory specimens were maintained in separate chambers in water tables.

Specimens not treated as above were fixed in 10% buffered formalin immediately after collection. After 24 to 48 hours they were rinsed with fresh water and transferred to 70% EtOH for storage. If buccal contents were to be examined, 1.0% Rose Bengal, by weight, was added to the alchohol in order to facilitate identification of organic materials (Bilyard, 1974; Shimek, 1988).

Scaphopod shells were measured (Shimek, 1989) and the soft parts removed for analysis of buccal contents as described by Bilyard (1974). All buccal pouch contents were enumerated and measured. Measurements taken varied with shape of the food items. The measurement was typically made along the semimajor axis, i.e. the second longest measurement. (During feeding the longest dimension of the prey, the major axis, is oriented normal to the plane of the buccal opening, thus the maximum distention of the buccal opening has to accommodate the second longest dimension of the prey.) Prey items were identified using available works (Cockbain, 1963, Lankford and Phegler, 1973; Gallagher, 1979; Kozloff, 1987).

Buccal pouch clearance rates were determined by periodic observation of living specimens. Immediately upon return to the laboratory, live scaphopods were put onto clean substratum from their native habitat. This sediment was previously treated with fresh water for several days in order to kill resident infauna. The sediment was then placed in miniature aquaria held inside of larger aquaria within a flow-through sea-water system. Perforations in the bottoms of the the miniature aquaria were coverd with 63 μm mesh plastic screen. The tops of the smaller aquaria were held above the water level in the water table and running sea water was supplied to them.

Five specimens of a given species of scaphopod were put into each aquarium; only those that burrowed completely into the substratum were used to determine buccal clearance rates. Starting at 24 hours after collection, some species were removed from the substratum and fixed for later examination. Additional specimens were fixed at 6 hr intervals thereafter. All scaphopods in a given aquarium were removed simultaneously. The buccal pouch contents were examined as indicated above.

Substratum was analyzed for particle size distribution following the methods of Holme and McIntyre (1971). A modified wet-sieve method was used to determine particle sizes to 0.63 μm. The total silt-clay fraction was determined by evaporation and weighing, but was not partitioned further.

The sediment organic content was estimated by determination of total volatile solids. Approximately 25 g of sediment was dried in a tared, pre-oxidized, aluminum pan and total weight determined. The pan and sediment were then heated in a muffle furnace at 500°C for 24 hr. The sediment and pan were allowed to cool in a desiccator and re-weighed. The difference between the two weights was used as weight of the total volatile solids.

Potential prey items were isolated from paired replicate substratum subsamples taken from the 1l sample of quantitatively collected sediment. After sediment for particle size analysis was removed, the remaining material was homogenized by stirring with a small amount of added sea water. A small aliquot (40 to 90 ml) of the homogenate was removed and fixed in 10% sea-water buffered formalin with rose bengal added. After 24 hours, the samples were washed through a 63 μm mesh screen and stored in 70% ethanol until examination.

Sediment samples were examined at 10 to 40 diameters using a Wild M-5 stereomicroscope and all infauna were enumerated and measured. Foraminiferan tests were seen commonly, but were not identified, measured, or enumerated. Similarly, time constraints did not allow the numerous other fragmentary remains, e.g. molluscan shells, scaphopod shells, heart urchin spines, and polychaete setae, to be measured, even though these items contribute to the gut contents of some scaphopods. The potential food value of these items is unknown. Fine inorganic particles and fecal pellets, the most common non-animal constituents of the sediment, were not enumerated even though they were found in some buccal contents. The relative proportion of each taxon in the infauna or the buccal contents was calculated by dividing the number of individuals of a particular taxon by the total number of individuals in that sample.

For statistical comparisons, potential prey from a particular habitat were defined as all individuals of all taxa that had been found at least once as part of the dietary intake of a scaphopod. Thus, all foraminiferans were considered to be potential prey, as were all bivalves; polychaetes and nematodes were not.

Most statistical analyses were performed using STATGRAPHICS (STSC, 1986, 1987, 1988). For analyses of variance, proportions were transformed by arcsine square-root transformation to decouple the variance from the means (Sokal and Rohlf, 1981). [Proportions approximate binomial distributions and the variance is a function of the mean which introduces bias into the analysis of variance (ANOVA). The arcsine square-root transformation prevents this.] The Shannon-Wiener diversity index (H) and the evenness index (J) were calculated where applicable (Poole, 1974).

RESULTS

Stations sampled differed in depth (Table 1), particle size distribution and volatile solids content (Figs. 1, 2, Table 2). Particle size distribution and total volatile solids differed significantly among stations, although not seasonally within a single station (Table 2).

The number of quantitative grabs varied among stations. Nonetheless, sufficient samples were taken to adequately assess scaphopod abundances, which varied among and within stations by species (Table 3). More scaphopods were found per unit area at the Sandford Island station than at the other two sites. Here *Dentalium rectius* was numerically domi-

Table 1. Scaphopod study sites and collection areas in Barkley Sound, Vancouver Island, British Columbia.

A. Station M - Mayne Bay, Northeastern Corner of Barkley Sound.
Corners of the sample collection area: 48° 58.8' N, 125° 18.9' W; 48° 59.0' N, 125° 19.2' W; 48° 58.6' N, 125° 20.1' W; 48° 58.4' N, 125° 19.7' W.
Centroid of the sample collection area: 48° 58.7' N, 125° 19.5' W.
Depth range of the sample collection area: 35-40 m.

B. Station S - Off Sandford Island, in Imperial Eagle Channel.
Corners of the sample collection area: 48° 52.3' N, 125° 11.4' W, 48° 52.5' N, 125° 11.7' W, 48° 53.1' N, 125° 11.1' W, 48° 52.8' N, 125° 11.2' W.
Centroid of the sample collection area: 48° 52.7' N, 125° 11.4' W.
Depth range of the sample collection area: 75-80 m.

C. Station T - Trevor Channel, near Diana Island. Corners of the sample collection area: 48° 50.0' N, 125° 10.8' W, 48° 50.2' N, 125° 10.0' W, 48° 49.3' N, 125° 11.7' W, 48° 49.1' N, 125° 11.5' W.
Centroid of the sample collection area: 48° 49.7' N, 125° 11.0' W.
Depth range of the sample collection area: 30-110 m.

Table 2. Tests of significance of the differences in station sediment parameters.

Source of Variation	Sum of Squares	d.f.	Mean Square	F-ratio	P
A. Analysis of variance for proportional sediment weights (proportions are arcsine-square root transformed).					
Main Effects	13.931	13	1.072	136.352	<0.0001
Particle Size	13.794	8	1.724	219.396	<0.0001
Station	0.104	2	0.052	6.645	0.0017
Month	0.032	3	0.011	1.372	0.2533
2-Factor Interactions	2.786	46	0.061	7.705	<0.0001
Particle Size x Station	2.519	16	0.157	20.030	<0.0001
Particle Size x Month	0.253	24	0.011	1.341	0.1463
Station x Month	0.014	6	0.002	0.296	0.9382
Residual	1.226	156	0.008		
Total	17.942	215			
B. Analysis of variance for proportional total volatile solids (proportions are arcsine-square foot transformed).					
Main Effects	2.966	13	0.228	8.544	<0.0001
Grain Size	2.753	8	0.344	12.886	<0.0001
Station	0.175	2	0.087	3.272	0.0405
Month	0.038	3	0.013	0.478	0.6981
2-Factor Interactions	3.936	46	0.086	3.204	<0.0001
Grain Size x Station	1.663	16	0.104	3.891	<0.0001
Grain Size x Month	1.759	24	0.073	2.745	0.0001
Station x Month	0.514	6	0.086	3.208	0.0053
Residual	4.166	156	0.027		
Total	11.068	215			

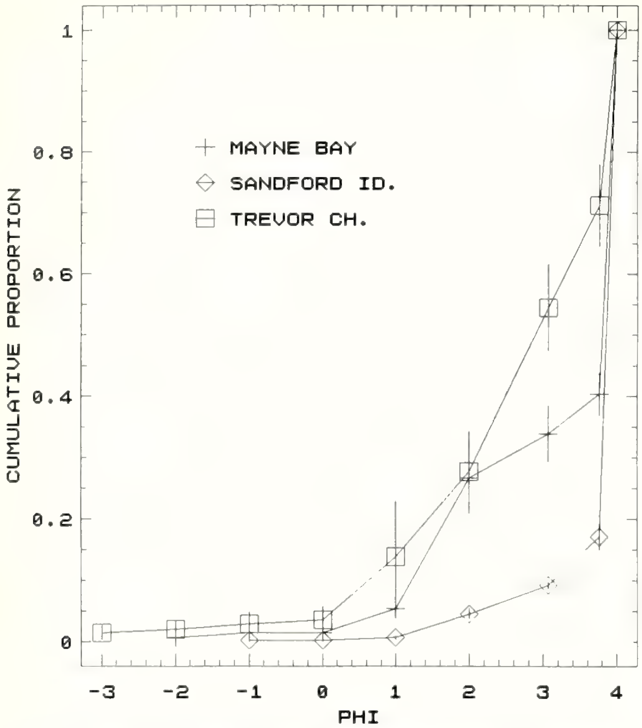

Fig. 1. Sediment particle size frequency distribution for all habitats, means ± 1 standard deviation indicated [Phi = $-\log_2$ (sediment particle diameter)].

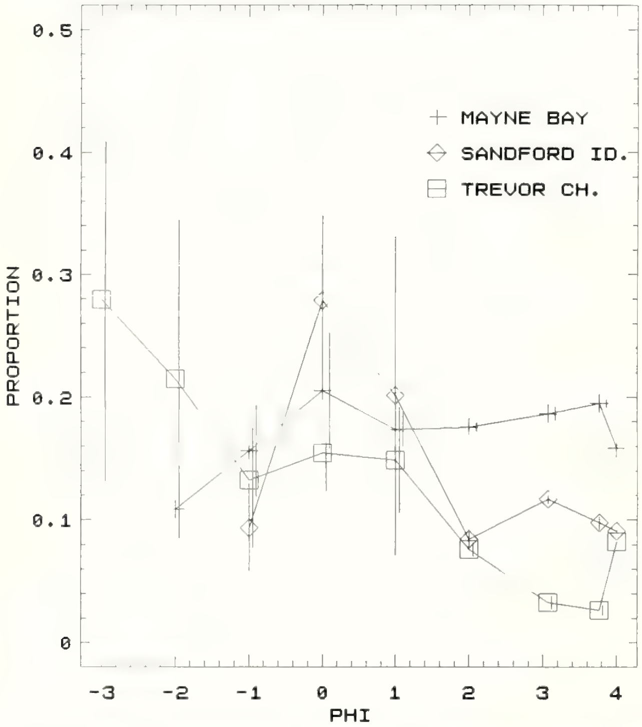

Fig. 2. Sediment total volatile solids by phi unit distribution for all habitats, means and 95% confidence intervals indicated. To avoid overlap, the confidence interval bars are displaced 0.10 phi units to the right for the Mayne Bay data and 0.05 phi units to the right for the Trevor Channel data (Phi = $-\log_2$ (sediment particle diameter)].

nant, averaging almost 60 animals/m^2; *Cadulus aberrans* was rarely collected.

Although the Mayne Bay and Trevor Channel sites had similar scaphopod densities, the species assemblages were significantly different. *Pulsellum salishorum* was found in similar abundances at all three sites. *Cadulus aberrans* was absent at the Mayne Bay site and relatively abundant at the Trevor Channel site. *Dentalium rectius* was about 12.5 times as abundant as the Mayne Bay site than at the Trevor Channel site.

Buccal contents were examined from 87 *Cadulus aberrans*, 231 *Dentalium rectius* and 149 *Pulsellum salishorum*. The proportion of each taken with food in the buccal pouch varied substantially (Table 4). A total of 2511 items were found among the buccal contents in *C. aberrans*, 654 in *D. rectius* and 603 in *P. salishorum*. *C. aberrans* and *P. salishorum* buccal contents consisted mainly of live, dead, or fragmental remains of foraminiferans. *D. rectius* buccal contents contained a large proportion of other items (Table 4). Both the diversity and the evenness of the dietary array of *D. rectius* were higher than in the other two species (Table 4).

Cadulus aberrans buccal contents contained 47 groups of items, mostly foraminiferans, with foraminiferan test fragments the third most common item (Table 4, Appendix Table 1). Five species of foraminifera accounted for over 80% of the total buccal contents (Appendix Table 1). The common prey species, *Cribrononion lene* (Cushman and McCulloch, 1940), *Elphidiella hannai* (Cushman and Grant, 1927), *Florilus basispinatus* (Cushman and Moyer, 1930), *Rosalina columbiensis* (Cushman, 1925), and *Buliminella exilis* (Brady, 1884), were also well represented in the diets of *Dentalium rectius* (Appendix Table 2) and *Pulsellum salishorum* (Appendix Table 3). Only 1.71% of *C. aberrans* buccal contents were other than foraminiferans.

Whole *Cribrononion lene* and Foraminifera fragments dominated the buccal contents of *Pulsellum salishorum*, accounting for almost 54% of the diet, a much larger proportion as compared to *Cadulus adherens* (Table 4, Appendix Table 3). Nevertheless, 29 other categories of dietary items were also found. Non-foraminiferan food categories, e.g. mineral grains, sediment boluses, mite eggs, and fecal pellets, constituted 8.79% of the total buccal contents (Appendix Table 3).

The buccal contents of *Dentalium rectius* included a broader array of items. While *Cribrononion lene* was the most common prey, 53 other categories of items were found (Table 4). In decreasing order, sediment particles, mite eggs, and fecal pellets were the three next groups constituting the buccal contents, cumulatively accounting for 30.89% of the diet (Appendix Table 2). In addition to 20 species of live foraminiferans, buccal pouch contents included substantial diversity in other food categories: live bivalves, ostracods, kinorhynchs, mites, barnacle cyprids, mite eggs, clear unidentified eggs, turbellarians, and gastropod eggs (Appendix Table 2). Non-living dietary components included polychaete setae, echinoid [*Brisaster latifrons* (A. Agassiz, 1898)] ossicles, ostracod valves, bivalve valves, blue polypropylene rope fragments, and several unidentified annulated objects (Appendix Table 2).

Infauna varied significantly among the stations, but not seasonally within each station (Tables 5-7). Those infauna found in the substratum were also well represented in the diets of scaphopods, indicating that the samples were an adequate assessment of prey availability. Several infauna taxa, particularly polychaetes, nematodes, amphipods, and harpacticoid copepods, were absent totally from the diet (Appendix Tables 1-3).

The dominant prey taxon was within the protistan Order Foraminiferida. Foraminiferans were present in the samples from all the localities sampled and were most abundant at the Trevor Channel site (Table 5). Foraminiferans were typically numerically dominant at all sites, although order of abundance varied (Tables 6, 8). Arenaceous forams, i.e. *Rheophax* sp., *Saccammina* sp., and *Haplophragmoides* sp., were typically more common at the silty Mayne Bay and Sandford Island sites, while overall foraminiferan species richness was greater at the Trevor Channel station (Table 8). Living foraminiferans were commonly eaten by all three scaphopod species (Appendix Tables 1-3) with *Cribrononion lene* as the most common prey of all three species of scaphopods, although its relative proportion varied widely. Similarly, the rank order and proportional abundances of the other five species of foraminiferans also varied. Thus, the most common live prey items for all three species of scaphopods studied here were typically one of the six common foraminiferans. The only other common living dietary items found in any scaphopod were mite eggs that were eaten relatively frequently by *Dentalium rectius* (Appendix Table 2).

An ANOVA of the arcsine transformed relative habitat and buccal content prey taxa proportions showed that these proportions varied significantly among predator species (Table 9). The proportions of all live prey taken by scaphopods were compared to the proportions of those same taxa found in each habitat and were found to differ significantly for all habitats (Table 9). The diet and habitat proportions of the major prey taxa were most similar at the Mayne Bay site (Fig. 3), intermediate at the Sandford Island site (Fig. 4), and least similar at the Trevor Channel site (Fig. 5).

Table 3. Scaphopod abundances as determined by quantitative sediment collection.

	Cadulus aberrans	*Dentalium rectius*	*Pulsellum salishorum*	All Scaphopods
A. Mayne Bay				
Sample size	10	10	10	10
Mean ± 1 S. E.	0.00 ± 0.00	18.00 ± 4.16	6.00 ± 2.67	24.00 ± 4.52
B. Sandford Island				
Size	8	8	8	8
Mean ± 1 S. E.	2.50 ± 1.64	58.75 ± 5.15	6.25 ± 2.63	67.5 ± 5.26
C. Trevor Channel				
Sample size	7	7	7	7
Mean ± 1 S. E.	5.71 ± 4.29	1.43 ± 1.43	10.00 ± 3.78	17.41 ± 5.65

Table 4. Summary of all buccal pouch contents.

	Cadulus aberrans			*Dentalium rectius*			*Pulsellum salishorum*		
	Taxa	Number	Percent	Taxa	Number	Percent	Taxa	Number	Percent
A. Buccal pouch items									
Live foraminiferans	28	1913	76.19	22	252	38.53	17	357	59.20
Foraminiferan tests	12	216	8.60	8	65	9.94	5	53	8.79
Other items	6	43	1.71	23	296	45.25	8	80	13.27
Foraminiferan fragments	1	339	13.5	1	41	6.27	1	113	18.74
Total	47	2511		54	654		31	603	
Mean number of items		29.2			4.5			5.9	

B. Proportion of scaphopods with food in buccal pouches.

	C. aberrans	*D. rectius*	*P. salishorum*
Number examined:	87	231	149
Number with buccal contents:	86	144	102
Proportion:	0.989	0.623	0.684

C. Dietary diversity.

	C. aberrans	*D. rectius*	*P. salishorum*
Shannon-Weiner (H')	2.406	2.926	2.329
Evenness (J)	0.625	0.734	0.678

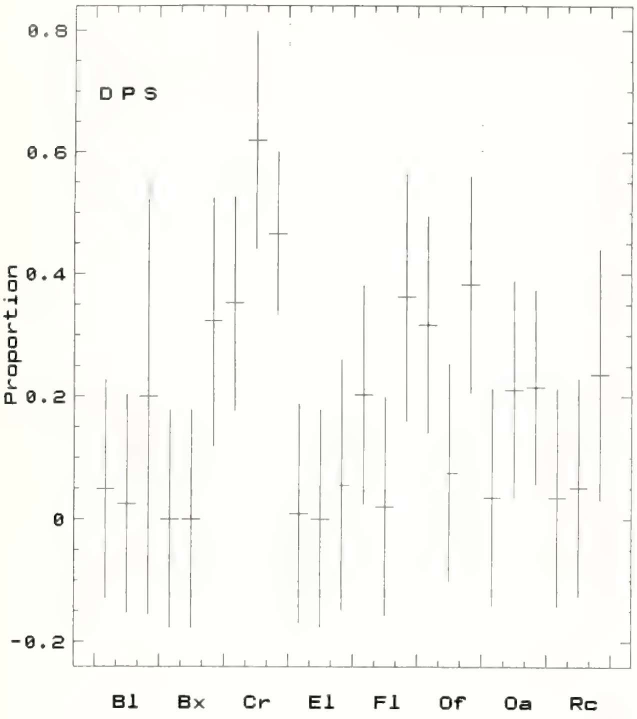

FIG. 3

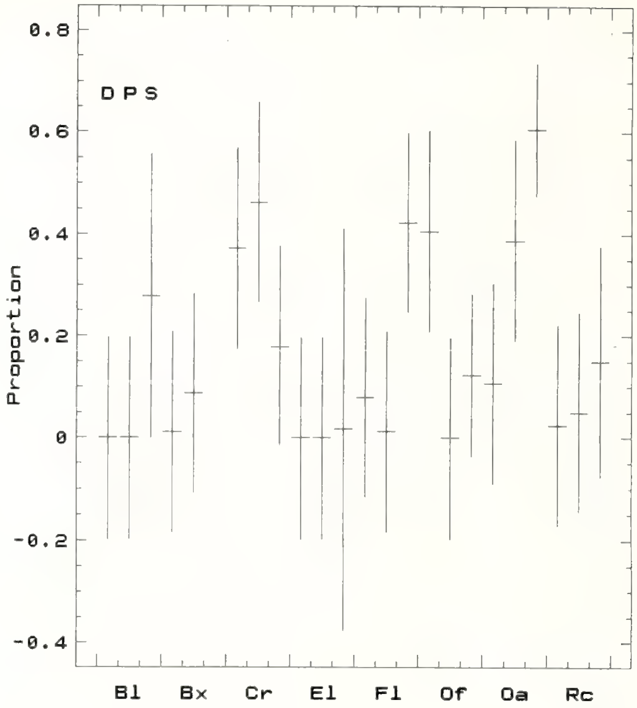

FIG. 4

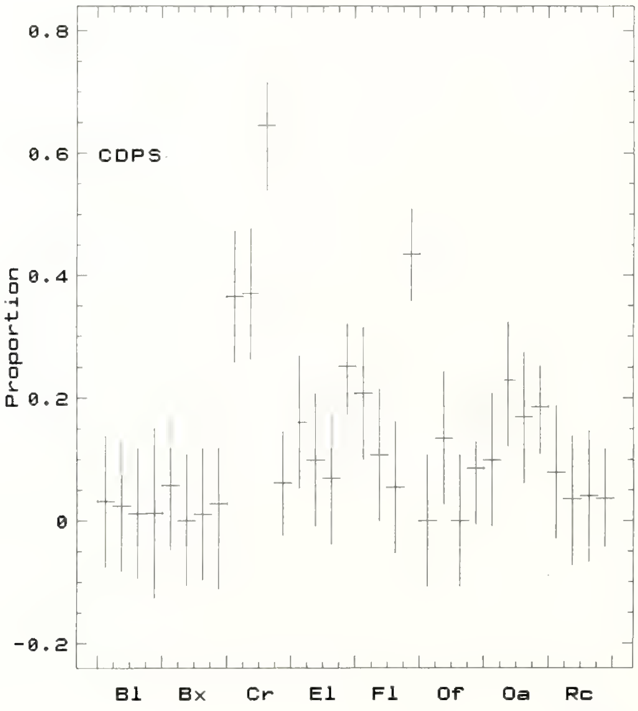

FIG. 5

Figs. 3-4. Proportions of prey species in the sediment and the diet; means and 95% confidence intervals indicated. The prey taxa are delimited by the vertical dashed lines. Each prey taxon has three bars indicating, from left to right, the relative proportions of that taxon in the buccal pouches of *Dentalium rectius,* D; *Pulsellum salishorum,* P; and the proportion of those taxa in the sediment, S. The prey taxa are: *Buliminella elegantissima,* Bl; *B. exilis,* Bx; *Cribrononion lene,* Cr; *Elphidiella hannai,* El; *Florilus basispinatus,* Fl; all other foraminiferans, Of; other animals, Oa; *Rosalina columbiensis,* Rc. Fig. 3, Mayne Bay; Fig. 4, Sandford Island. **Fig. 5.** As for Figs. 3-4 except each prey taxon now has 4 vertical bars, the farthest left bar indicating the relative proportions of that taxon in the buccal pouches of *Cadulus aberrans,* C. Trevor Channel.

The relative mean dietary prey proportions of *Dentalium rectius* and *Pulsellum salishorum* at Mayne Bay and Sandford Island sites were not significantly different from one another (Table 10). At the Trevor Channel site, the mean dietary prey proportions for all three scaphopod species could be grouped together as significantly different from the habitat proportions of those same prey taxa. Alternatively, the mean prey proportions for *Cadulus aberrans, D. rectius* and the habitat form a group not significantly different from one another, but different from the mean prey proportions found in *P. salishorum* (Table 10).

Patterns of prey utilization emerged when the dietary and habitat proportions were compared over all habitats for each major prey species by month and habitat. Proportional abundances of all major prey taxa or items differed significantly between the habitat and the buccal contents of at least one of the scaphopod species. These differences were consistent and not due to seasonal or other habitat variations (Table 11).

Buliminella elegantissima was found in the gut contents of all of scaphopods significantly less frequently than in the associated habitats (Fig. 6). *B. exilis* was found in the guts of *Dentalium rectius* and *Pulsellum salishorum* significantly less frequently than in the associated substratum (Fig. 7). Although the mean proportional abundance of *B. exilis* in *Cadulus aberrans* buccal contents was less than the habitat, the difference was not significant (Fig. 7).

Summed over all the habitats, the mean proportional abundances of *Cribrononion lene* in the substratum and buccal contents of all the scaphopods did not differ significantly (Fig. 8). In Mayne Bay site populations of *Dentalium rectius* and *Pulsellum salishorum;* however, the mean proportional buccal abundances of *C. lene* were significantly greater than in the habitat (Fig. 3).

Elphidiella hannai and *Rosalina columbiensis* were found significantly less frequently in the guts of *Dentalium rectius* and *Pulsellum salishorum* than in the sediments, while *Cadulus aberrans* ate them in about the same proportion as found in the habitats (Figs. 9, 10). A similar pattern was seen for *Florilus basispinatus*; the buccal abundances were less but not significantly so in *C. aberrans* (Fig. 11).

Halacaridan eggs were not eaten regularly by either *Cadulus aberrans* or *Pulsellum salishorum*. The eggs were taken in about the same proportion as they were found in the environment by *Dentalium rectius* (Fig. 12).

There was no difference between the sizes of foraminiferan and non-foraminiferan prey eaten by *Dentalium rectius* (Fig. 13). Although *D. rectius* could eat items only marginally smaller than the size of its ventral shell aperture, the majority of the diet consisted of smaller particles and organisms (Fig. 13).

The size-frequency distributions of the buccal contents of *Dentalium rectius* (Fig. 14) and *Pulsellum salishorum* from the Mayne Bay site (Fig. 15) did not differ significantly from each other. The means of the pooled size-frequency distributions of ingested foraminiferans were significantly smaller than those from the habitat (Fig. 16), as were the buccal contents (Figs. 17, 18). The same is true for foraminiferans from the Sandford Island site (Fig. 19). At both stations, relatively more small prey were ingested by scaphopods than were collected from the habitat, nevertheless, these patterns are only subtly different (Figs. 16, 19).

Table 5. Potential prey in Barkley Sound.

A. Abundance of foraminiferans.

Habitat	Number of Samples	Foraminiferans/ml Mean ± 1 Standard Error
Mayne Bay	10	0.18 ± 0.08
Sandford Island	10	0.27 ± 0.12
Trevor Channel	10	2.17 ± 0.41

B. ANOVA - differences in the number of foraminiferans /ml of sediment.

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	P
Habitat	25.168	2	12.584	19.686	<0.001

At the Trevor Channel site, all scaphopod buccal contents show a preponderance of smaller prey items, the semi-major diameter typically less than 300 μm (Figs. 20-22). The pattern of prey size utilization is similar in all three scaphopod species. The habitat foraminiferan size frequency distribution at this station is quite different than either of the other two stations or the buccal contents of any of the predators (Fig. 23). Of particular interest at this station is the predominance of predation by *Cadulus aberrans* in regulating the prey size frequency distribution. *C. aberrans* ingested so many foraminiferans that their cumulative distribution is effectively that of *C. abberans* prey; the regulatory contributions of both *Dentalium* and *Pulsellum* were minor.

No scaphopods studied here show a significant relationship between changes in ventral aperture width and the size of dietary items found in the buccal pouch (Table 12). The data are highly scattered, therefore the r-squared valules are exceedingly low and the regressions given here represent the best fit from several different models. The regressions were calculated on a seasonal basis for *Cadulus aberrans* prey, because of the large sample sizes (Table 12). The minor differences in the slope and intercept of the regression lines were not significantly different, and no line has a slope significantly different from zero. None of the regressions for any scaphopod species differed significantly from any other (Table 12).

Scaphopods processed prey at different rates. *Dentalium rectius* and *Pulsellum salishorum* completely cleared their buccal pouches within 36 hours. *Cadulus aberrans* took over 3 days to utilize all the items in their buccal pouches (Fig. 24). The buccal pouch contents of *C. aberrans*; however, were much more numerous, and individual foraminiferans were actually processed at a greater rate.

DISCUSSION

HABITATS

The three Barkley Sound sites differed significantly in particle size distribution and proportion of total volatile solids,

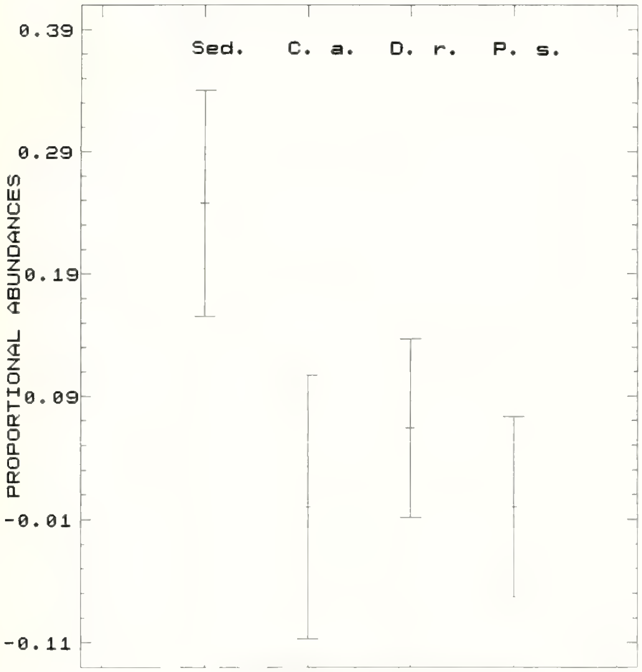

FIG. 6

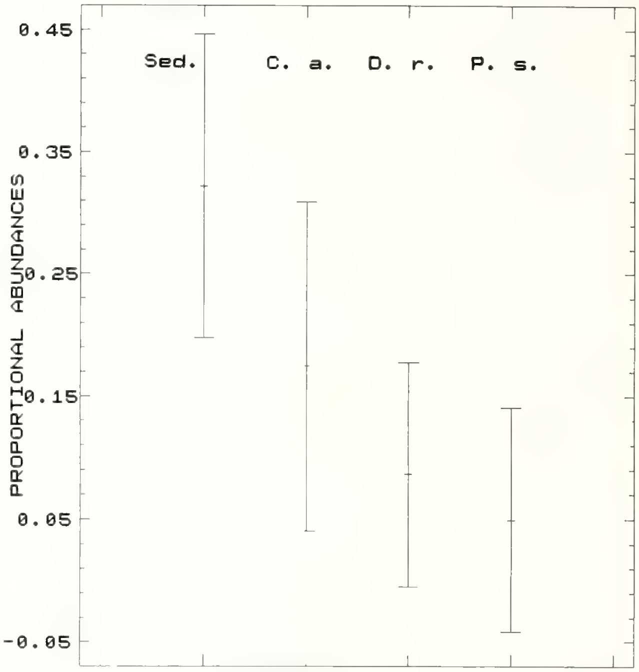

FIG. 7

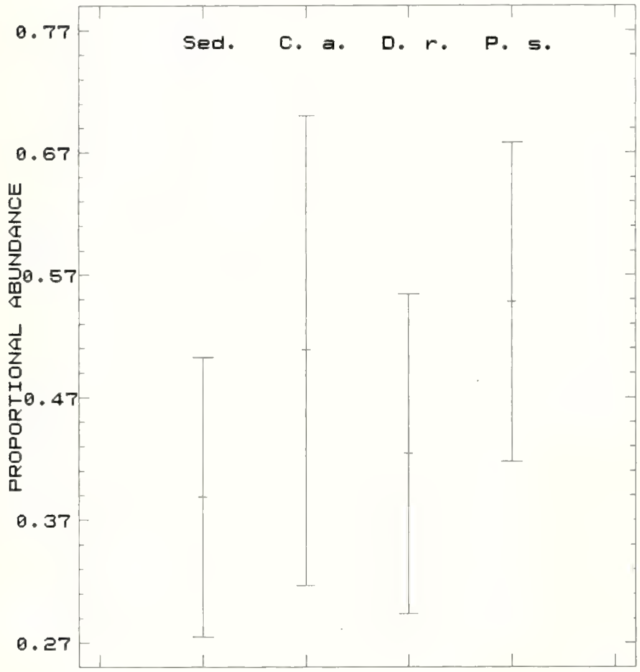

FIG. 8

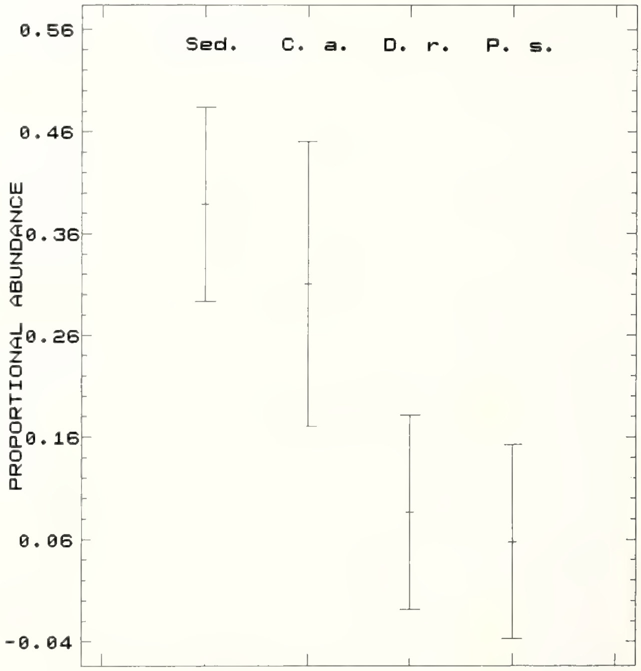

FIG. 9

Figs. 6-9. Mean proportional abundance of individual prey pooled for all habitats and in the buccal pouches of all the scaphopod species. Mean abundances and 95% confidence intervals of arcsine transformed proportional abundances are shown (sediment, Sed; *Cadulus aberrans,* C.a.; *Dentalium rectius,* D.r.; *Pulsellum salishorum,* P.s.) Fig. 6, *Buliminella elegantissima;* Fig. 7, *B. exilis;* Fig. 8, *Cribrononion lene;* Fig. 9, *Elphidiella hannai.*

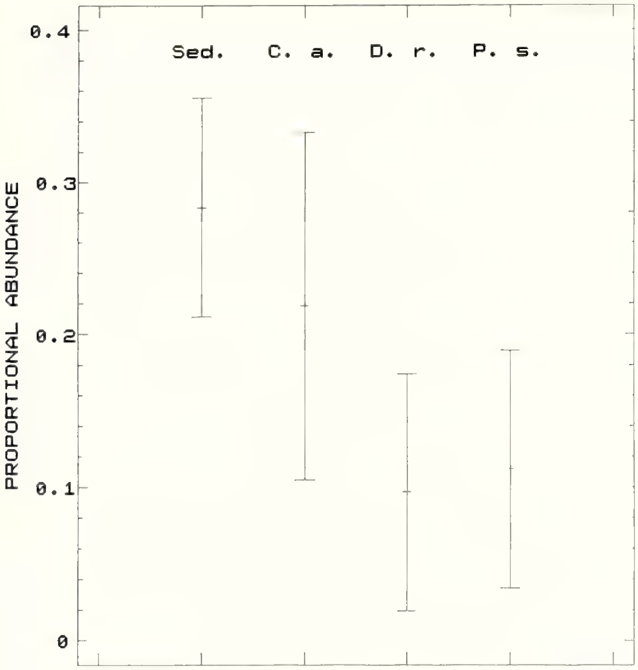

FIG. 10

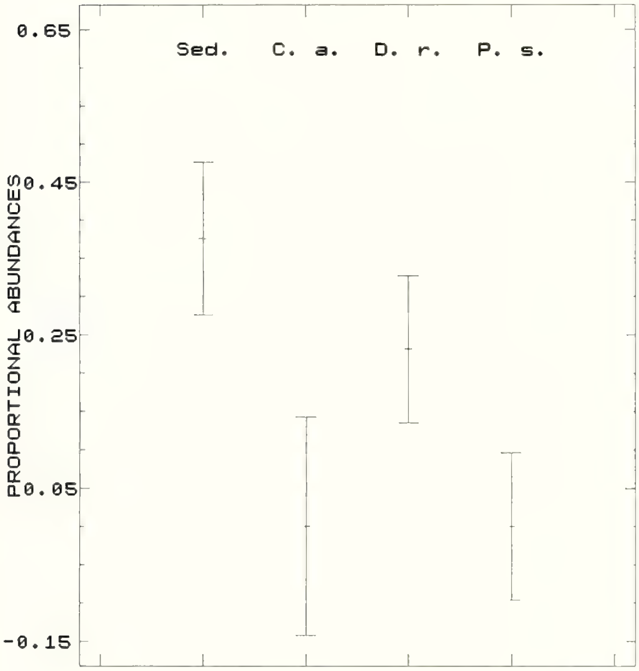

FIG. 12

although neither varied significantly from month to month (Table 2, Fig. 1). The Sandford Island site had a significantly higher silt fraction than did either of the other sites; the Trevor Channel site had the smallest silt fraction. The Mayne Bay site fraction was intermediate, but more similar to that of the Sandford Island site.

Thomson (1981) indicated that the organic content of the substratum along Barkley Sound ranges from about 20% (by weight) in the northeast to about 5% in the southwest. The stations sampled here are consistent with that account (Table 2, Fig. 2).

The relationship of sediment particle size distributions and the total volatile solids found at the three stations was complex. The proportion of coarser sediment (smaller phi sizes) varied substantially. A consistent hierarchy was evident; however, in sediment fractions smaller than 250 μm (phi ≥ 2). The Mayne Bay site had more volatile solids than did the Sandford Island site, which in turn had more than the Trevor Channel site. Most of the particles at each station were also smaller than 250 μm (Fig. 1), thus the trend was consistent among stations.

The relatively high proportion of coarse organic particles at the Trevor Channel site (Fig. 2) is due to substantial kinetic energy input during storms. As a result coarse algal material is ground into the substratum. Observations taken from the submersible PISCES IV confirmed large laminarian kelp fragments on, and partially ground into, the substratum at depths exceeding 90m. Judging by the relative paucity of total volatile solids in the smaller particle size fractions, it is likely these larger particles are being broken down and utilized relatively rapidly, probably as food for infaunal organisms. The infauna at this station were both more diverse and abundant than at the other two sites (Tables 5, 6).

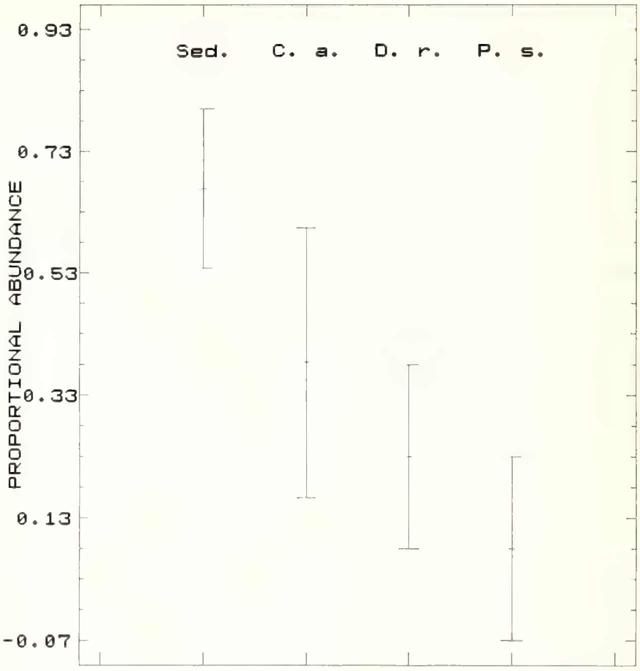

FIG. 11

Figs. 10-12. Mean proportional abundance of individual prey pooled for all habitats and in the buccal pouches of all the scaphopod species. Mean abundances and 95% confidence intervals of arcsine transformed proportional abundances are shown (sediment, Sed; *Cadulus aberrans*, C.a.; *Dentalium rectius*, D.r.; *Pulsellum salishorum* P.s.). Fig. 10, *Rosalina columbiensis;* Fig. 11, *Florilus basispinatus;* Fig. 12, Halacaridan mite eggs.

Table 6. Infauna collected.

A. MAYNE BAY

Month/Year	12/83	12/83	3/84	3/84	6/84	6/84	9/84	9/84	12/84	12/84	Total collected
Number of samples	1	2	1	2	1	2	1	2	1	2	
Volume (ml)	35	40	40	61	93	71	59	56	58	56.5	
FORAMINIFERA											
Astrorhizidae sp.				1							1
Buliminella elegantissima										3	3
B. exilis					2				7	4	13
Cribrononion lene	8	6	1			2		1	3	5	26
Elphidiella hannai	1	1							1		3
Florilus basispinatus	17	5							1		23
Lagena sp. A	1										1
Nonionella stella									1		1
Rheophax sp.									1		1
Rosalina columbiensis					2				4	2	8
Saccammina					1	2					3
OTHER INVERTEBRATES											
Mite eggs				3				1	2	1	7
Kinorhynch sp.									2		2
Polychaete sp.	6										6
Amphipod sp.	1										1
Nematode sp.	1										1
Harpacticoid sp.	2								4		6
Axinopsida serricata											10
Ophiuroid sp.		1									1
Ostracod sp.									1		1
TOTAL	37	23	1	4	5	4	0	2	27	15	118

B. SANDFORD ISLAND

Month/Year	12/83	12/83	3/84	3/84	6/84	6/84	9/84	9/84	12/84	12/84	Total Collected
Number of samples	1	2	1	2	1	2	1	2	1	2	
Volume (ml)	57	65	58	44	69	85	54	62.5	59	58.5	
FORAMINIFERA											
Astrorhizidae sp.			1	3							4
Buliminella elegantissima									15	24	39
Cibicides sp.									1		1
Cribrononion lene						2		3	2	3	10
Elphidiella hannai									1		1
Florilus basispinatus		2	1				5		4	7	19
Globobulimina	2						1		9	6	17
Haplophragmoides sp.					1						1
Hippocrenella sp.									1		1
Lagena sp. A	1								1		2
L. sp. B					1						1
L. sp. D									1		1
L. sp. E									2		2
Nonion sp.								3	4	11	18
Nonionella stella								2	2	7	11
Rosalina columbiensis						4			1	4	9
Rheophax sp.					6	1					7
Rotorbinella sp.									2		2
Saccammina sp.						2			5	4	11
Spirulina sp.			1	2					2		5
Textularia sp.									2		2
Triloculina sp. A	1										1
OTHER INVERTEBRATES											
Mite eggs				1	1	1	2		2	1	8
Kinorhynch sp.									1	4	5
Ostracod sp.			1		2					2	5
Polychaete sp.			1								1
Nematode sp.			2	1					3	100	106
Corophium sp.									1		1
Harpacticoid sp.										6	6
TOTAL	3	2	7	7	11	10	8	8	62	179	297

Table 6. (continued)

	C. TREVOR CHANNEL										
Month/Year	12/83	12/83	3/84	3/84	6/84	6/84	9/84	9/84	12/84	12/84	Total Collected
Number of samples	1	2	1	2	1	2	1	2	1	2	
Volume (ml)	59	65	56	52	59	69	57	49.5	52.5	39.8	
FORAMINIFERANS											
Astrorhizidae sp.			2								2
Astrononion sp.						1	1		1		3
Buliminella sp. C									1		1
B. sp. D									1		1
B. elegantissima								1	4	1	6
B. exilis							1		15	2	18
Cibicides sp.							4		3		7
Cribrononion lene	3			2	2	7	13	5	16	9	57
Discorbinella sp.							1				1
Elphidiella hannai	6	8	37	47		70	2	20	99	12	301
Faujacina sp.				5	1	4	10	2	3		25
Florilus basispinatus	144	72	34	26	60	60	15	15	57	30	513
Globobulimina sp.	8	4	4	2	2	4			4	6	34
Haplophragmoides sp.				3		1	8			2	14
Lagena sp. A		1									1
L. sp. B			1			1	1				3
L. sp. C			1		1	1	1				4
L. sp. D						1					1
Nonion sp. D							1		5		6
Nonionella stella							2	1	4	2	9
Quinqueloculina sp.									1		1
Rosalina columbiensis		1	2	5	3	4	1	8	2	3	29
Rheophax sp.							1		3	4	8
Rotorbinella sp.							1	3	3		7
Saccammina sp.										1	1
Spirulina sp.			1		1				9	47	58
Textularia sp.			1			3		1	4		9
Triloculina sp. A	1	4	3						6	2	16
T. sp. B		2		1		3			1		7
T. sp. C		1				1			2	2	6
T. sp. D									1		1
Unidentified Foraminiferan									1		1
Uvigerina sp.			1			3	5		1	3	13
OTHER INVERTEBRATES											
Axinopsida serricata						2			4		6
Compsomyax subdiaphana			2	2					1	47	52
Mytilus sp.					1						1
Mite eggs			3				1				4
Kinorhynch sp.										3	3
Ostracod sp.			2	2		1	2		7	29	43
Harpacticoid sp.									2		2
Nematode sp.								1		10	11
Tanaid (*Leptochelia*?)									4	1	5
Corophium sp.									2		2
TOTAL	162	93	93	95	71	167	71	57	268	216	1293

Scaphopod abundances sampled here were much higher than hitherto reported from other areas (Gainey, 1972; Bilyard, 1974). These high abundances are not rare; however, dredging reports from other fjord systems on Vancouver Island indicate similar scaphopod abundances in deeper areas (W. Austin, pers. comm.). High scaphopod densities probably occur in all silty fjord environments of Northern British Columbia and Southeastern Alaska.

It is likely that the scaphopod abundances documented here (Table 3) reflect substantial underestimates of total abundances. These data were based on samples taken by Petersen grabs, which typically penetrate the bottom only to a depth of 15 to 20 cm (Holme and McIntyre, 1971). Laboratory obser-vatons made here and observations by Poon (1987) and J. Levitt (pers. comm.), confirm that the scaphopods studied here are capable of burrowing to a depth of up to 30 to 40 cm in aerobic substrata (Shimek, 1988, 1989). The depth of the redox discontinuity is unknown from stations studied here, but exceeds the sampling depth; no samples had indication of anaerobiosis. I believe actual scaphopod densities to be two to five times higher than these reported here.

INFAUNA

The sample size for the infaunal examination was adequate to determine abundances of common taxa at the Mayne Bay and Sandford Island sites, but was less reliable in regard to uncommon taxa. Sample sizes at the Trevor Channel site were sufficiently large to determine all infaunal abundances.

No seasonal trends in infaunal abundances could be demonstrated at any station (Tables 6, 7), although this could be an artifact of the variance introduced by relatively small foraminiferan sample sizes from the Mayne Bay and Sandford Island sites. However, no statistically significant changes were found at the Trevor Channel site.

Infaunal abundances did differ significantly among the three sites. This is best seen in the foraminiferan abundances although similar trends in other taxa can be seen as well (Tables 5, 6, 7, 8). Although the foraminiferans were generally dominated by the same group of species at all stations, the rank order and proportional abundances did vary.

Differences in prey abundances can be related to scaphopods in one of two ways: 1) scaphopods passively tracked prey populations with regard to their diets, which would be evident if they had the same relative proportions of any given prey in their guts as were found in the native substratum; 2) scaphopods could be altering the distributions of their prey. The latter condition would be supported if there was evidence of active selection or rejection of individual prey.

POTENTIAL PREY

The ANOVA on the proportional abundances of the common prey were sufficiently robust to demonstrate significant variation in the foraminiferan abundance among habitats (Table 5). In addition, the major prey taxa abundances differed significantly in all of the habitats, but not from month to month, or between the taxa seasonally (Table 7). The pattern of variation and the significance of the interactive terms was similar from all three areas, indicating the samples tracked consistent patterns throughout the Barkley Sound area.

Previous studies (Lacaze-Duthiers, 1856, 1857; Morton, 1959; Pilsbry and Sharp, 1897-98, Dinamani, 1964; Fisher-Piette and Franc, 1968; Gainey, 1972; Bilyard, 1974; Carter, 1983; Poon, 1987) indicated the major prey of scaphopods were foraminiferans. Consequently, I examined the variation in foraminiferan abundances in detail. At all sites foraminiferans numerically dominated the infaunal communities. Although organisms smaller than 63 μm were regularly found in scaphopod gut contents, substrata examined for infauna were sieved with a 63 μm screen to remove silt and clay. Therefore, potential prey size-frequency data are reliable only for size classes greater than 63 μm. Organisms less than 10 μm in diameter were not analyzed and it is likely bacteria and small eukaryotic organisms were quite abundant. These organisms comprise food for foraminiferans, and contribute directly to the diet of the deposit-feeding *Dentalium rectius*. Abundances of microorganisms can be only inferred.

DIETS

Previous observations on scaphopod diets have been based either on small data sets generated from relatively few individuals from one population (Gainey, 1972; Bilyard, 1974; Taib, 1980; Poon, 1987) or various species (Carter, 1983). With the exception of Bilyard (1974) and Poon (1987), the taxonomic precision of the dietary determinations has been inadequate for detailed analysis. Bilyard (op. cit.) recognized selection and rejection of potential dietary items by *Dentalium entale stimpsoni* Henderson, 1920. Poon (op. cit.) also found restricted diets in *Cadulus tolmiei.* The diets reported here are consistent with their observations: the scaphopods studied herein selectively accept or reject individual food items (Shimek, 1988).

The prey collected from scaphopod buccal pouches represented a diverse array of whole organisms and other items. All scaphopods preyed on foraminiferans. However, the relationships of these and other prey taxa varied significantly among the predator species (Table 4, Appendix Tables 1-3). Additionally, while buccal contents differed significantly from area to area, seasonal variations were insignificant (Figs. 3-5; Table 9).

CADULUS ABERRANS

This species fed in accordance with stereotypical scaphopods, specializing on live foraminiferans which were numerically dominant, although empty foraminiferan tests and test fragments also comprised a substantial fraction of the prey (Table 4). *Cadulus aberrans* also fed more frequently: 98.9% of individuals had prey in the buccal pouches, and had more food items in their buccal pouches (mean = 29.2) than did either of the other species. Total prey number could be high: one individual had 135 items in its buccal pouch.

The size of the predator, as measured by ventral aperture width, was not related to the size of the prey. No significant changes in the sizes of the buccal contents occurred with the seasons.

Prey composition varied; however, five species of live foraminiferans and foraminiferan fragments comprised over 80% of the diet (Appendix Table 1). Dietary diversity was low (H' = 2.406) but higher than that of the other foraminiferan predator *Pulsellum.* The evenness index (J = 0.625) was the lowest of all scaphopods studied indicating the numerical dominance of those few prey taxa (Table 4).

PULSELLUM SALISHORUM

This species also preyed mostly upon live foraminiferans, although dead foraminiferan remains constituted a substantially larger component of their diets than in *Cadulus aberrans*. Live *Cribrononion lene* dominated the diet with empty foraminiferan tests next most common.

Foraminiferan tests, like other particulate mineral matter in benthic ecosystems, become colonized by bacteria. These tests, therefore, can be desirable food sources; bacteria have a relatively high nitrogen to carbon ratio (Dales, 1964; Meadows, 1964). In addition, the tests could be an important dietary source at calcium carbonate for scaphopods in silty environments.

About 42% of the total buccal contents, 256 items, consisted of live *Cribrononion lene.* The rest of the seven most common dietary categories were dead items and together with *C. lene* represented over 80% of total buccal contents (Appendix Table 3). Selection for a single prey type was reflected

Table 7. Analysis of variance to test for differences in proportional prey abundances.

Source of variation	Sum of squares	d.f.	Mean square	F-ratio	P
		MAYNE BAY			
MAIN EFFECTS	4.526	10	0.453	5.506	<0.0001
Prey taxon	4.342	7	0.620	7.545	<0.0001
Month sampled	0.197	3	0.066	0.797	0.5001
2-FACTOR INTERACTIONS					
Taxa by months	1.861	21	0.089	1.078	0.3940
RESIDUAL	5.014	61	0.082		
TOTAL	11.401	92			
		SANDFORD ISLAND			
MAIN EFFECTS	5.645	10	0.564	4.282	0.0001
Prey taxon	5.530	7	0.790	5.992	<0.0001
Month sampled	0.095	3	0.032	0.241	0.8678
2-FACTOR INTERACTIONS					
Taxa by month	2.093	21	0.100	0.756	0.7600
RESIDUAL	9.229	70	0.132		
TOTAL	16.968	101			
		TREVOR CHANNEL			
MAIN EFFECTS	4.891	10	0.489	9.632	<0.0001
Prey taxon	4.859	7	0.694	13.670	<0.0001
Month sampled	0.036	3	0.012	0.239	0.8690
2-FACTOR INTERACTIONS					
Taxa by months	1.038	21	0.049	0.973	0.4995
RESIDUAL	7.464	147	0.051		
TOTAL	13.390	178			

in the Shannon-Wiener Index (H' = 2.329), which was lower for this species than the other two scaphopods studied here.

Only 68.4% of *Pulsellum salishorum* had buccal pouch contents which averaged 5.9 prey items per individual, far fewer than in the other foraminiferan specialist, *Cadulus aberrans*, and more than *Dentalium rectius* (Table 4). No seasonal or habitat patterns in feeding were seen. Nor were any patterns evident regarding the relative sizes of predator and prey. *P. salishorum* was about equally abundant in all three habitats sampled. This could reflect the lack of foraminiferan prey at the Mayne Bay and Sandford Island sites, and competition from the more active and voracious *C. aberrans* at the Trevor Channel site.

DENTALIUM RECTIUS

Only 62% of *Dentalium rectius* contained food in the gut, averaging 4.54 prey items per individual. The diet was also more evenly distributed among the other categories of prey items (J = 0.734), as compared to *Cadulus aberrans* and *Pulsellum salishorum* (Table 4). Again, no significant patterns relating predator and prey sizes were evident, probably due to the high variability in prey.

Although *Cribononion lene* was the most common live prey organism, most of the buccal pouch contents did not consist of live foraminiferans (Table 4, Appendix Table 2, Fig. 13). Sediment, compacted into small boluses, was also commonly ingested, as were fecal pellets, mineral sediment grains, and foraminiferan fragments. The surfaces of these items could be sources of bacteria which probably constitute a major food source for this species. Sediment and mineral grains have been noted in the diets of *Dentalium entalis* L. (1980) and *D. stimpsoni* (Bilyard, 1974), although little significance has been attached to these items as sources of nutrition. Bright gold-colored eggs presumed, by comparison, to be halacarid mite eggs, were the second most commonly ingested food item of *Dentalium rectius.*

Dietary diversity was greater (H' = 2.93) than that of either of the other two species of scaphopods. Of the organisms collected from the substrata, only polychaetes, nematodes, and harpacticoid copepods were not found in the gut of at least one specimen of *Dentalium rectius.* It is likely these animals move rapidly or vigorously enough to avoid capture by captacular attachment.

The captacular morphology of *Dentalium rectius* allows collection of fine particulate material. This mode of feeding is well documented among dentalioid scaphopods (Dinamani, 1964; Gainey, 1972; Bilyard, 1974; Shimek, 1988). The wide array of dietary items eaten by *D. rectius* reflects the effectiveness of this feeding mode. Several types of very fine particulate matter were commonly in the form of boluses in the buccal pouches. In addition, many of the mineral grains, foraminiferan fragments, small uniloculate foraminiferans, and unidentified black spherules (diameters to 30 μm) could also have been collected by the captacular ciliary band.

Many of the prey of *Dentalium rectius* were not capable of rapid or sustained motion, as were virtually none of the prey

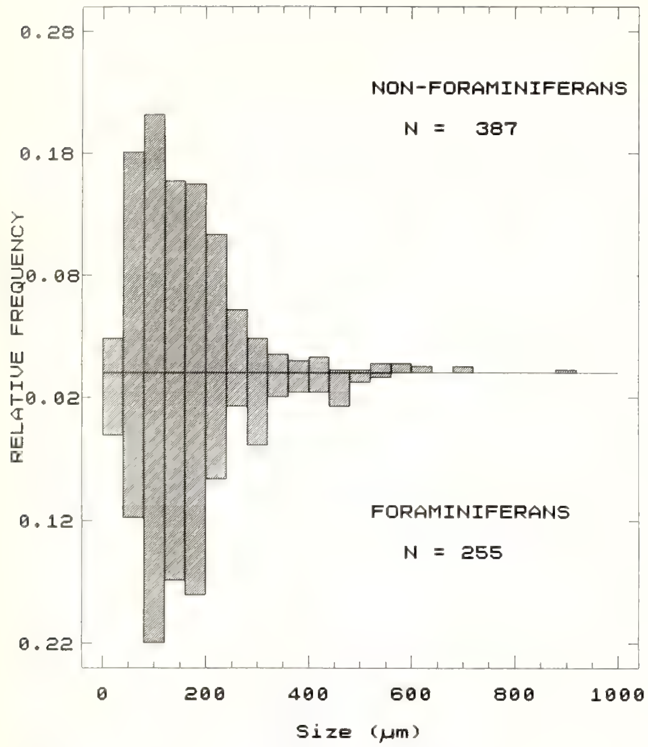

Fig. 13. Size frequency distribution of *Dentalium rectius* buccal contents, pooled over all habitats. The mean ± 1 standard deviation for the non-foraminiferan distribution = 170 ± 116µm, for the foraminiferan distribution = 174 ± 103 µm. The computed t statistic for the difference in the means: t = -0.419; P = 0.675, not significant; α = 0.05.

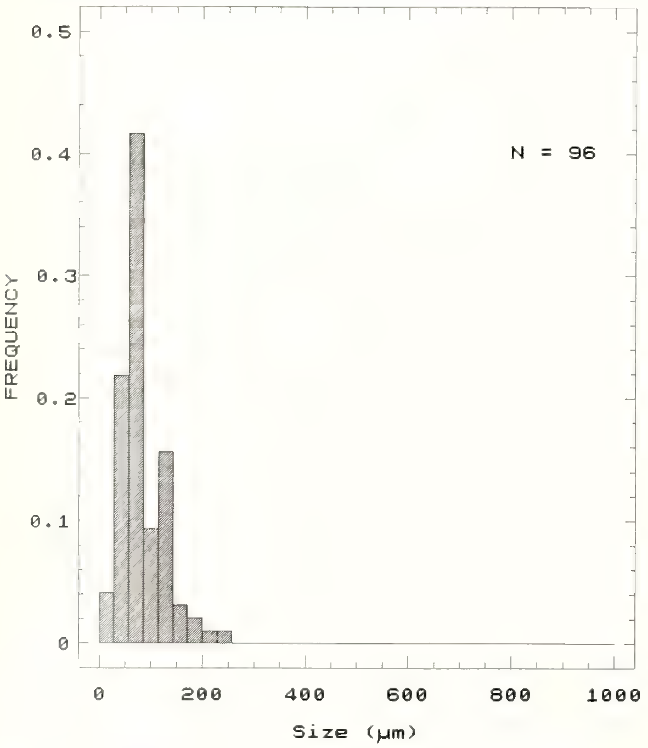

Fig. 15. Mayne Bay. Size frequency distribution of *Pulsellum salishorum* buccal contents.

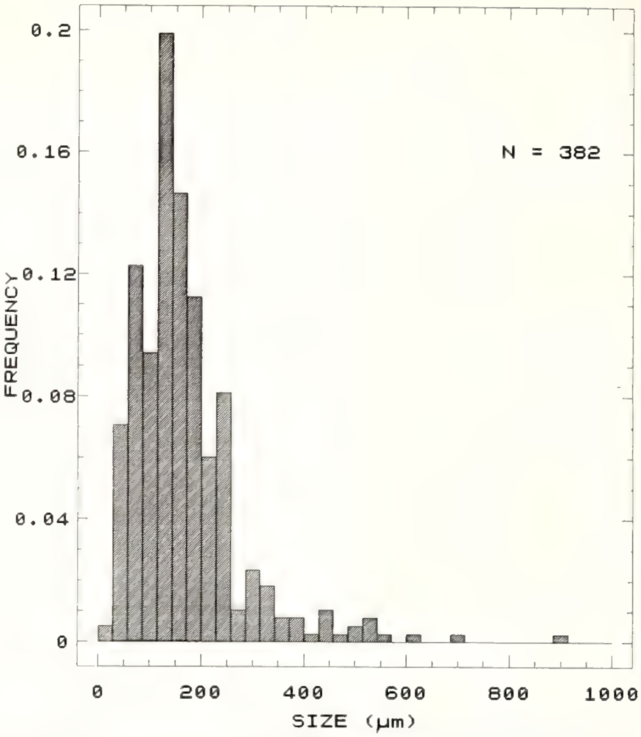

Fig. 14. Mayne Bay. Size frequency distribution of *Dentalium rectius* buccal contents.

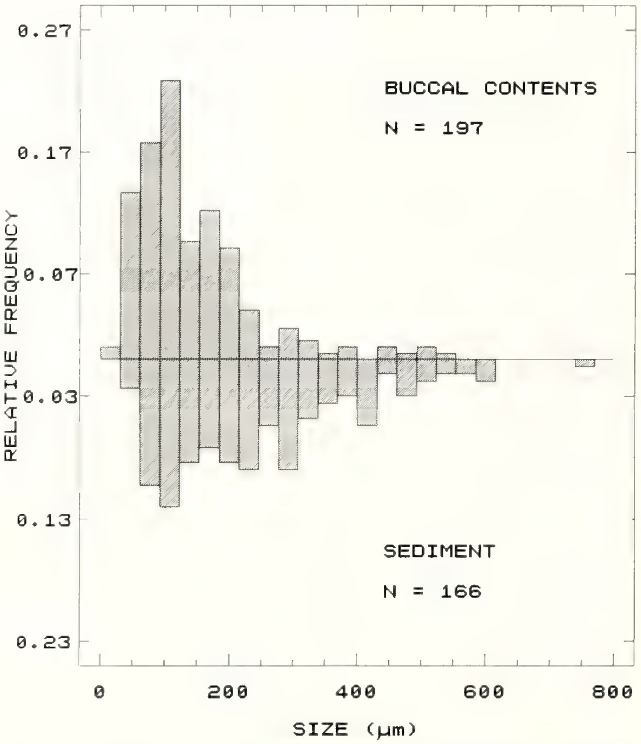

Fig. 16. Mayne Bay. Size frequency distribution of sediment and buccal content foraminiferans. Buccal content foraminiferans are pooled over all scaphopods. The mean ± 1 standard deviation for the sediment foraminiferan distribution = 245 ± 143 µm; for the buccal foraminiferan distribution = 142 ± 93 µm. The computed t statistic for the difference in means: t = -8.226; P = 9.922 x 10^{-9}, highly significant; α = 0.05.

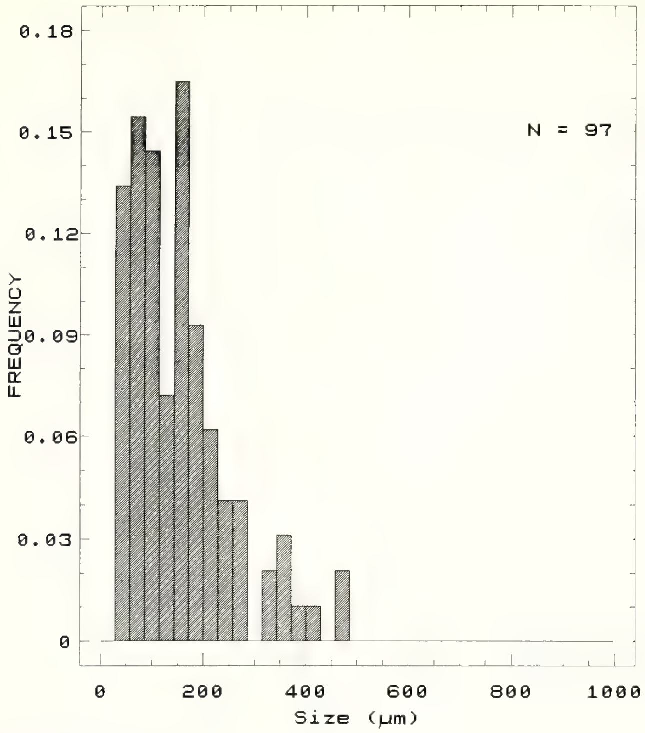

Fig. 17. Sandford Island. Size frequency distribution of *Dentalium rectius* buccal contents.

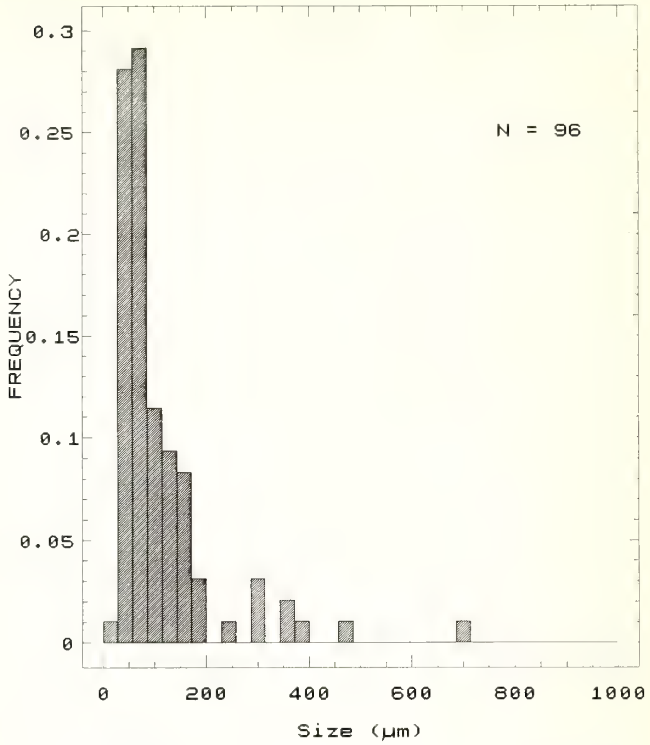

Fig. 18. Sandford Island. Size frequency distribution of *Pulsellum salishorum* buccal contents.

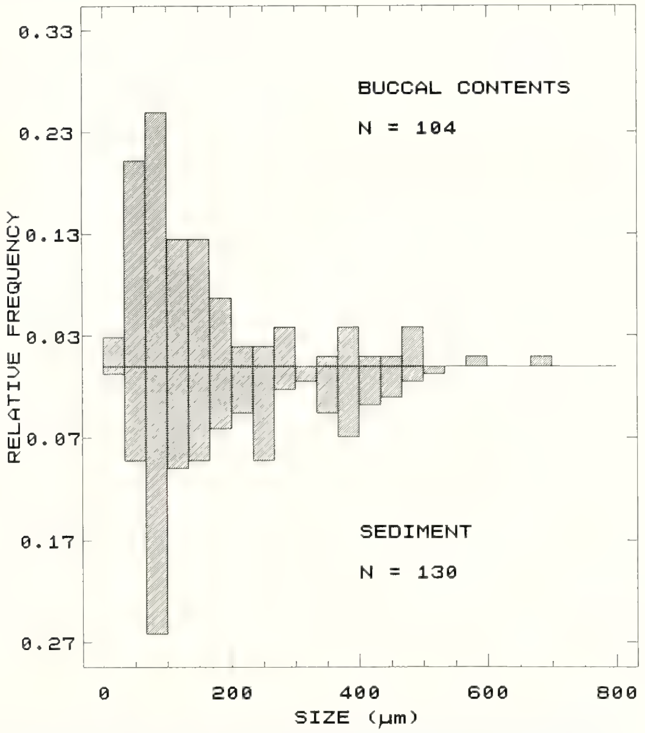

Fig. 19. Sandford Island. Size frequency distribution of sediment and buccal content foraminiferans. Buccal content foraminiferans are pooled over all scaphopods. The mean ± 1 standard deviation for the sediment foraminiferan distribution = 190 ± 128 μm; for the buccal foraminiferan distribution = 154 ± 134 μm. The computed t statistic for the difference in the means: t = -2.090; P = 0.0377, significantly different; α = 0.05.

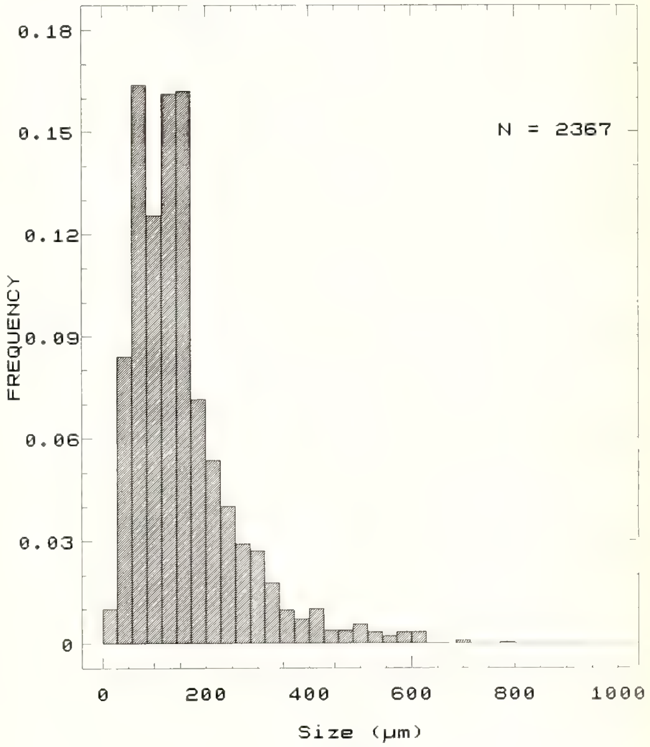

Fig. 20. Trevor Channel Site. Size frequency distribution of *Cadulus aberrans* buccal contents.

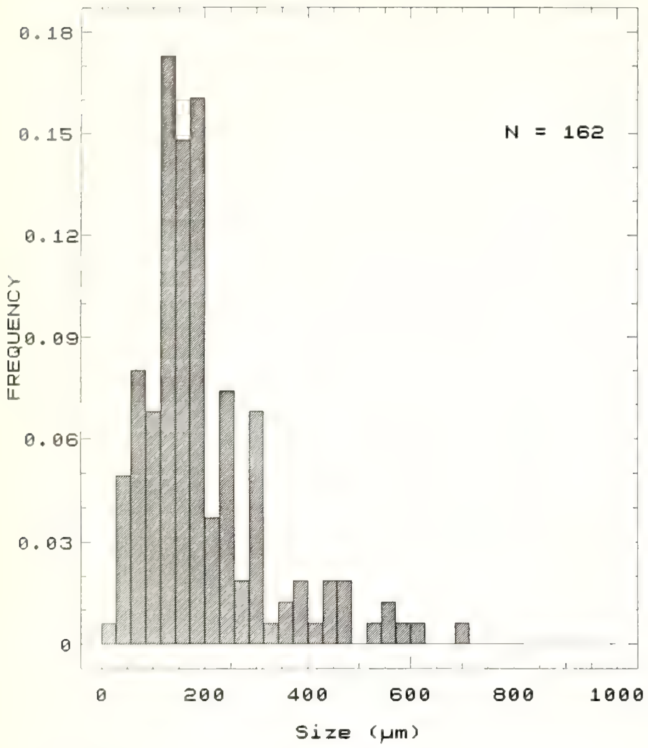

Fig. 21. Trevor Channel Site. Size frequency distribution of *Dentalium rectius* buccal contents.

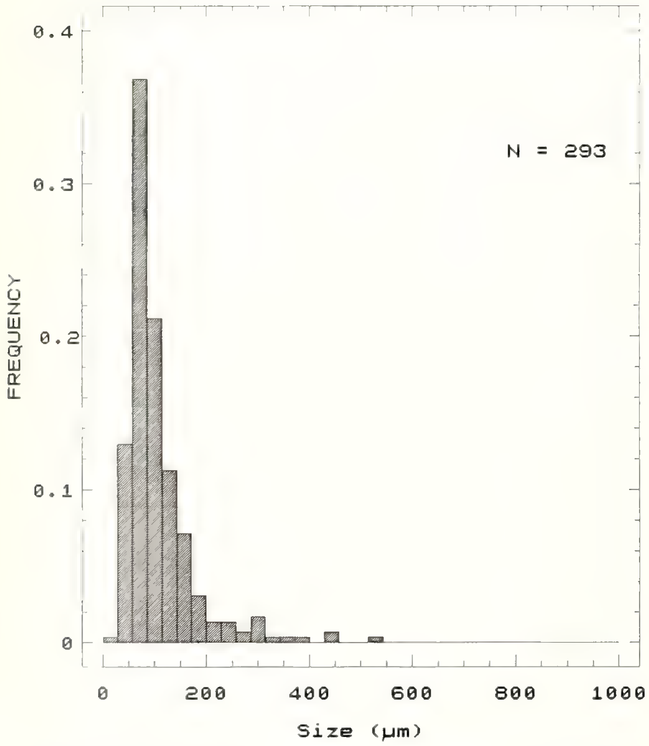

Fig. 22. Trevor Channel Site. Size frequency distribution of *Pulsellum salishorum* buccal contents.

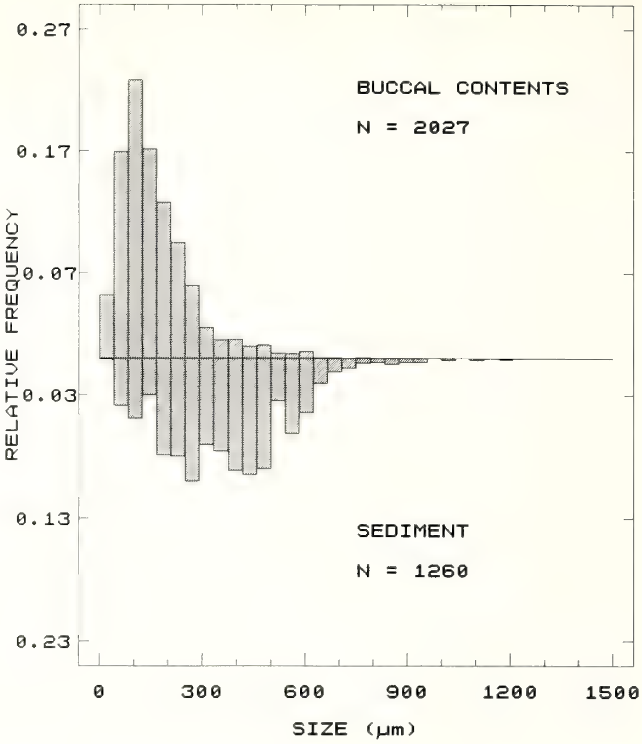

Fig. 23. Trevor Channel Site. Size frequency distribution of sediment and buccal content foraminiferans. Buccal content foraminiferans are pooled over all scaphopods. The mean ± 1 mean standard deviation for the sediment foraminiferan distribution = 368 ± 177 µm; for the buccal foraminiferan distribution = 163 ± 106 µm. The computed t statistic for the difference in the means: $t = -41.419$; $P = 1.010 \times 10^{-7}$, highly significant; $\alpha = 0.05$.

of either *Cadulus aberrans* or *Pulsellum salishorum.* Nevertheless, at least occasionally, a few relatively mobile prey were caught. These included ostracods, a barnacle cyprid, a mite, and several kinorhynchs. Their susceptibility to predation could be caused by properties of their cuticles or their lack of vigorous directed locomotion.

PREY SPECIALIZATION BY TAXON

All three species ingested items that appear to have little nutritive value. Bilyard (1974) found that *Dentalium entale stimpsoni* ate few empty foraminiferan tests. By calculating electivities he (Bilyard, op. cit). concluded empty tests were not desired food items. Empty foraminiferan tests and test fragments are found commonly in the sediment and in the buccal contents of all three species of scaphopods examined here.

It is possible to assess selectivity of predation within the foraminiferan component of the total dietary array by comparing proportional prey abundances. If the proportional abundances found in the buccal pouches approximated the proportional abundances for the same taxon in the native habitat, then the scaphopods were harvesting the foraminiferans as they were encountered. If the abundances in the buccal pouches were greater than in the habitat, the scaphopods were presumably actively selecting prey items. If the abundances of the foraminiferans in the gut were less than found in the native substratum, the scaphopods were presumably actively rejecting these potential prey.

The most abundant foraminiferans found in the scaphopod buccal pouches were also among the most common foraminiferan taxa in the habitat, although in some cases other species were more abundant (Appendix Tables 1-3, Tables 6-8). All foraminiferans, and the halacarid mite eggs, were designated as "potential food items" and their abundances were examined at each habitat on a seasonal basis. These abundances were significantly different from one another, but the relative proportional abundances did not vary significantly among seasons in any habitat examined (Table 7). Because these taxa did not vary significantly seasonally, the data were pooled over all the sampling periods, and the proportional abundances of these taxa were calculated (Table 8). Pooling had the effect of increasing the effective sample size for the Mayne Bay and Sandford Island sites infauna, possibly ameliorating the problems of foraminiferan rarity.

The ANOVA of the relative prey proportions in the habitat or buccal contents had three components (Table 9). The first test indicated significant differences among the potential prey taxa; they were not equally abundant. The second test indicated, except at the Trevor Channel site, significant differences in the pooled abundances of potential prey from the habitat and buccal contents. The two-factor interaction tested for significant differences in the relative abundances of foraminiferans between the predators' diets and the sediment for each habitat. In all cases the two-factor tests showed highly significantly differences in proportional abundances (Table 9).

The pattern of these proportional abundance differences was similar for all habitats (Table 10). At Mayne Bay and Sandford Island sites, *Dentalium rectius* and *Pusellum salishorum* had mean proportional prey abundances that were not significantly different from one another, but the relative proportion of potential prey was significantly less in their buccal contents than in the habitats; the predators were not ingesting foraminiferans at a frequency equal to the number of encounters. At the Trevor Channel site, all three scaphopods followed a similar pattern; however, the mean relative proportional abundances of each foraminiferan species found in the substratum was lower. This was likely an artifact of the increased foraminiferan diversity at this site, coupled with the lack of dominance of any one species. Thus, typically any potential foraminiferan prey was part of a larger species array than at the other two stations, and constituted a proportionally smaller fractional component of the fauna. The relative proportional abundances of *Cadulus aberrans* and *D. rectius* prey items, and the potential prey from the habitat are not significantly different from one another. Habitat and potential prey abundances do differ for *P. salishorum*. Likewise prey abundances did not differ significantly among the three scaphopods but they did differ from the respective sediment abundances (Table 10).

Therefore, at the Trevor Channel site, the lower mean proportional abundances of potential prey in the sediment coupled with the diverse diet of *Cadulus aberrans* make the differences less distinct. However, the mean proportional abundances of foraminiferans in buccal contents of the three scaphopods are significantly lower than those found in the sediment, a pattern identical to those of the other two areas (Table 10).

Table 8. Habitat foraminiferan abundances as a proportion of the total enumerated prey.

Species	Mayne Bay	Sandford Island	Trevor Channel
Astrononion sp.	—	—	0.011
Astrorhiza sp.	0.004	0.019	0.011
Buliminella elegantissima	0.049	0.154	0.018
B. exilis	0.228	0.142	0.102
B. sp. C	—	—	0.011
B. sp. D	—	—	0.011
Cibicides sp.	—	0.013	0.013
Cribrononion lene	0.227	0.067	0.053
Discorbinella sp.	—	—	0.010
Elphidiella hannai	0.017	0.012	0.134
Faujacina sp.	—	—	0.017
Florilus basispinatus	0.196	0.079	0.223
Globobulimina sp.	0.012	0.069	0.038
Haplophragmoides sp.	—	0.003	0.013
Hippocrenella sp.	—	0.004	—
Lagena sp. A	0.007	0.008	0.011
L. sp. B	—	0.003	0.011
L. sp. C	—	—	0.011
L. sp. D	—	0.013	0.011
L. sp. E	—	0.007	—
Nonion sp. D	—	0.066	0.012
Nonionella stella	0.016	0.127	0.024
Quinculoculina sp.	—	—	0.011
Rheophax sp.	0.051	0.022	0.014
Rosalina columbiensis	0.124	0.076	0.025
Rotorbinella sp.	—	0.007	0.013
Saccammina sp.	0.009	0.039	0.015
Spirillina sp.	—	0.030	0.042
Textularia sp.	0.012	0.037	0.028
T. sp. B	—	—	0.012
Triloculina sp. A	0.012	0.004	0.021
T. sp. B	—	—	0.014
T. sp. C	—	—	0.013
T. sp. D	—	—	0.011
Uvigerina sp.	—	—	0.021
Unidentified	0.037	—	0.014

This prey utilization pattern indicates that scaphopods typically rejected most of the potential food items that they encountered. Detailed examination of the six most abundant foraminiferans found in the buccal pouches, as well as utilization of halacarid mite eggs, reveals different patterns for the utilization of each major prey taxon (Table 11).

Buliminella elegantissima was eaten less frequently than expected by all three scaphopod species (Table 11, Fig. 6). A different pattern was shown by *B. exilis* and *Florilus basispinatus,* which were preyed upon significantly less frequently by *Dentalium rectius* and *Pulsellum salishorum.*

Table 9. Comparison of the arcsine transformed prey proportional abundances from the habitat and scaphopod buccal contents.

Source of variation	Sum of squares	d.f.	Mean square	F-ratio	P
MAYNE BAY					
MAIN EFFECTS	5.678	9	0.631	10.407	<0.0001
Prey taxon	3.461	7	0.494	8.156	<0.0001
Source (habitat or buccal contents by species)	1.349	2	0.674	11.123	0.0001
2-FACTOR INTERACTIONS					
Taxa by source	1.541	14	0.110	1.815	0.0535
RESIDUAL	4.183	69	0.061		
TOTAL	11.402	92			
SANDFORD ISLAND					
MAIN EFFECTS	6.515	9	0.724	8.576	<0.0001
Prey taxon	3.819	7	0.546	6.463	<0.0001
Source (habitat or buccal contents by species)	1.093	2	0.546	6.472	0.0026
2-FACTOR INTERACTIONS					
Taxa by source	3.039	13	0.234	2.769	0.0031
RESIDUAL	5.993	71	0.084		
TOTAL	15.547	93			
TREVOR CHANNEL					
MAIN EFFECTS	5.002	10	0.500	16.945	<0.0001
Prey taxon	4.636	7	0.662	22.437	<0.0001
Source (habitat or buccal contents by species)	0.147	3	0.049	1.661	0.1779
2-FACTOR INTERACTIONS					
Prey and source	4.052	21	0.193	6.538	<0.0001
RESIDUAL	4.339	147	0.030		
TOTAL	13.393	178			

Although the mean proportions of these prey species in the buccal contents *Cadulus aberrans* were less than expected, the difference was not statistically significant (Table 11, Fig. 7, 11).

Table 10. Multiple range tests of the pooled prey abundances as a proportion of the total potential prey abundances from the sediment and the buccal contents of each scaphopod species examined. Homogeneous groups, indicated by the same letter, do not have significantly different mean proportional prey abundances.

Source	Mean proportional prey abundances	Homogeneous groups	
MAYNE BAY			
Pulsellum salishorum	0.224	A	
Dentalium rectius	0.259	A	
Sediment	0.573		B
SANDFORD ISLAND			
P. salishorum	0.218	A	
D. rectius	0.255	A	
Sediment	0.599		B
TREVOR CHANNEL			
P. salishorum	0.255	A	
D. rectius	0.283	A	B
Cadulus aberrans	0.370		B

Elphidiella hannai and *Rosalina columbiensis* were ingested by *Cadulus aberrans* about as frequently as they were encountered. Both of these foraminiferans were ingested significantly less frequently by *Dentalium rectius* and *Pulsellum salishorum* (Table 11, Figs. 9, 11).

The mean proportion of *Cribrononoin lene* in buccal contents was higher than that in the sediment for all three scaphopod species, although the elevation for *Dentalium rectius* was minimal. None of the elevations was significant if the data were pooled over all the habitats (Table 11, Fig. 8). Occasionally in some habitats, the elevation was significant (Fig. 5).

Halacaridan egg predation provided an interesting contrast to that of foraminiferans (Fig. 12). The eggs were ingested slightly less frequently than they were encountered by *Dentalium rectius*. The eggs were rarely eaten by the other two scaphopods species. This difference was highly significant (Table 11).

Sufficient data were available to test for prey utilization differences on a seasonal basis for all major taxa except for *Buliminella* sp. No significant differences were found.

Some differences in proportional usage occurred between the habitats. For example, while pooled data indicated

Table 11. Analysis of variance for major prey arcsine transformed proportional abundances.

Source of variation	Sum of squares	d.f.	Mean square	F-ratio	P
Buliminella elegantissima					
MAIN EFFECTS					
Category (habitat, diet)	0.346	3	0.115	6.892	0.0009
RESIDUAL	0.603	36	0.017		
TOTAL	0.949	39			
Buliminella exilis					
MAIN EFFECTS					
Category (habitat, prey)	0.379	3	0.126	4.811	0.0066
RESIDUAL	0.919	35	0.026		
TOTAL	1.298	38			
Cribrononion lene					
MAIN EFFECTS	0.398	6	0.066	1.246	0.3088
Category (habitat, prey)	0.237	3	0.079	1.480	0.2379
Month	0.182	3	0.061	1.136	0.3489
2-FACTOR INTERACTIONS					
Category by months	0.211	9	0.023	0.440	0.9033
RESIDUAL	1.759	33	0.053		
TOTAL	2.368	48			
Elphidiella hannai					
MAIN EFFECTS	1.095	6	0.182	6.477	0.0002
Category (habitat, diet)	1.030	3	0.343	12.197	0.0000
Months	0.129	3	0.043	1.524	0.2293
2-FACTOR INTERACTIONS					
Category by months	0.275	9	0.031	1.085	0.4029
RESIDUAL	0.817	29	0.028		
TOTAL	2.186	44			
Florilus basispinatus					
MAIN EFFECTS	2.973	6	0.495	7.011	0.0001
Category (habitat, prey)	2.363	3	0.787	11.142	< 0.0001
Months	0.107	3	0.036	0.506	0.6811
2-FACTOR INTERACTIONS					
Category by monthws	0.199	9	0.022	0.313	0.9652
RESIDUAL	2.332	33	0.071		
TOTAL	5.504	48			
Rosalina columbiensis					
MAIN EFFECTS	0.358	6	0.060	3.183	0.0150
Category (habitat, prey)	0.295	3	0.098	5.237	0.0048
Months	0.40	3	0.013	0.703	0.5572
2-FACTOR INTERACTIONS					
Category by months	0.285	9	0.032	1.689	0.1341
RESIDUAL	0.582	31	0.019		
TOTAL	1.225	46			
Halacarid eggs					
MAIN EFFECTS	1.201	6	0.200	6.969	0.0001
Category (habitat, prey)	1.097	3	0.366	12.736	< 0.0001
Months	0.095	3	0.032	1.102	0.3647
2-FACTOR INTERACTIONS					
Category by prey	0.326	9	0.036	1.261	0.3005
RESIDUAL	0.804	28	0.029		
TOTAL	2.331	43			

that *Cribrononion lene* were eaten more frequently than expected, utilization rates were not significantly different between the habitat and the buccal contents. At the Trevor Channel site, however, all three species of scaphopods ate *C. lene* significantly more frequently than expected (Fig. 5).

PREY SPECIALIZATION BY SIZE

All three scaphopods ingested prey up to about 1.00 mm in semimajor axis diameter. The upper limit of prey size was effectively the ventral shell aperture diameter. The preponderance of all items ingested however, was less than 300 μm in diameter.

The ingested prey size-frequency distributions were consistent within each species across the habitats. The majority of the prey eaten by *Dentalium rectius* were smaller than 200 μm, nevertheless, a substantial portion of its diet was composed of larger items (Fig. 13, 14, 17, 21). The sizes of the foraminiferan and non-foraminiferan prey items did not differ significantly (Fig. 13).

Pulsellum salishorum ate smaller prey than the other scaphopods; most of its prey were smaller than 100 μm in diameter (Figs. 15, 18, 22), although prey size varied. *P. salishorum* is smaller than *Dentalium rectius* (Shimek, 1989), and the slight difference in the respective buccal content size-frequency distributions could be a reflection of this disparity. There were no significant increases in the size of the buccal contents with increases in the size of the ventral aperture of the scaphopod shell (Table 12).

The median prey size was taken by *Cadulus aberrans* at Trevor Channel site was between that of the other two species, although the total ranges broadly overlapped. Particularly between the two selective foraminiferan predators; however, the minor differences in the median sizes of prey eaten could be important in facilitating differential prey utilization. The mean adult ventral aperture width between these species did not differ (Shimek, 1989).

EFFECTS OF PREDATION

Without the results of experimental manipulation (Shimek, unpub. data), unambiguous determination of the result of scaphopod predation on the infauna is impossible. Nonetheless, circumstantial evidence suggested that significant effects are caused by this guild of infaunal predators. Both the mean sizes, and the size-frequency distributions of cumulative foraminiferan prey eaten, were significantly different from the mean sizes and size-frequency distributions of the foraminiferans collected from the habitat. This was especially notable at the Trevor Channel station where *Cadulus aberrans* seemed to exert substantial predation pressure on infaunal foraminiferans.

Although all three scaphopod species were found at this station, the number of the foraminiferans eaten by *Cadulus aberrans* was substantially greater. Also, processing of ingested prey occurred more rapidly in *C. aberrans* (Fig. 24). Nevertheless, the predatory effect was cumulative among all three scaphopods. The total size frequency distribution of the habitat foraminiferans at the Trevor Channel site was decidedly skewed to larger-sized individuals, while the cumulative buccal contents were skewed to smaller ones. One explanation of this shift involves selective and effective removal of most of the smaller prey by the predators. Similar patterns were also evident at the other stations but were based on smaller sample sizes; both the foraminiferan buccal contents, and habitat foraminiferans were less abundant at the Mayne Bay and Sandford Island sites (Figs. 16, 19, and 23).

Likewise, the effects of species-specific predation by the scaphopod predators appeared evident. Typically, the species that were most common in the habitat were not as commonly represented in the diets. With the case of *Florilus basisipinatus* and the *Buliminella* spp., this shift was particularly evident. The converse was notable with respect to *Cribrononion lene.* This species was the most abundant prey

Table 12. Regression analysis of ventral aperture width vs. prey size, linear model: Y = a+bX, no regression has a slope significantly different from 0.

	R-squared	Number
Cadulus aberrans		
March: Y = 122.13 + 56.313X	0.35	1282
June: Y = 195.30 − 48.347X	0.42	234
Sept.: Y = 291.69 − 128.198X	5.45	143
Dec.: Y = 103.83 + 9.876X	0.02	714
Dentalium rectius		
All: Y = 104.25 + 33.925X	3.04	642
Pulsellum salishorum		
All: Y = 14.672 + 83.296X	1.97	485

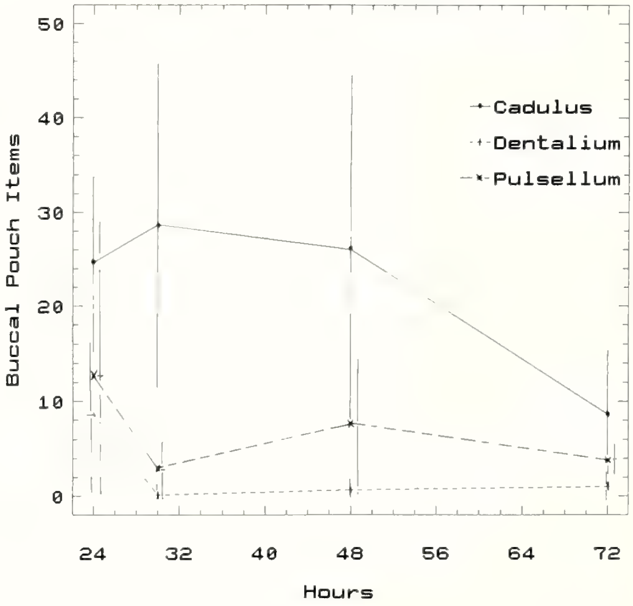

Fig. 24. The buccal pouch clearing times for all the scaphopod species; mean values ± 1 standard deviation are plotted. For clarity, the standard deviation bars are placed to the left of the times for *Dentalium rectius,* and to the right of the times for *Pulsellum salishorum.*

eaten (Appendix Tables 1-3), but was relatively uncommon in the habitats (Table 8). While it is tempting to attribute observed differences to scaphopod predation, and although I believe this to be the case, such a statement is premature prior to substantiation based upon experimental data.

ACKNOWLEDGMENTS

This work was supported in large part by the Bamfield Marine Station. I thank its former director, Dr. Ronald Foreman, for his friendly support and encouragement of this project. Additional and much welcomed financial support for data analysis was provided by the Pacific Northwest Shell Club. I thank Dr. Donald A. Thomson of the University of Arizona for providing necessary laboratory space and facilities during a portion of the data analysis. Parametrix, Inc. provided computer support.

Field assistance was provided by Anne Bergey, Janean Clark, James Dalby, Joel Elliott, Roxie Fredrickson, Tracy Geernaert, Sabina Leader, Armand Leroi, Steve Rumrill, Ross Warren, and, especially, the late Sigurd Tveit. I thank R. Fredrickson and Alan J. Kohn for thorough and rigorous criticisms of earlier drafts of this paper.

I dedicate this paper to Sigurd Tveit, a true Master of Ships, whose knowledge, skillful help, and friendship made difficult sampling a pleasure.

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Appendix Table 1. Gut contents of 87 *Cadulus aberrans* [86 (=98.9%) feeding].

Buccal Contents	Total	Percent	
		Item	Cumulative
Cribrononion lene	697	27.76	27.76
Elphidiella hannai	373	14.85	42.61
Foraminiferan fragments	339	13.50	56.11
Florilus basispinatus	336	13.38	69.49
Rosalina columbiensis	179	7.13	76.62
Buliminella exilis	99	3.94	80.57
R. columbiensis (test)	69	2.75	83.31
B. elegantissima	46	1.83	85.15
C. lene (test)	42	1.67	86.82
Mineral grains	31	1.23	88.05
B. exilis (test)	28	1.12	89.17
Nonionella stella	27	1.08	90.24
F. basispinatus (test)	26	1.04	91.28
Foraminiferan sp.	26	1.04	92.31
Textularia sp.	25	1.00	93.31
B. elegantissima (test)	24	0.96	94.27
Globobulimina sp. (test)	17	0.68	94.94
Triloculina sp.	17	0.68	95.62
Uvigerina sp.	16	0.64	96.26
B. sp. C	13	0.52	96.77
E. hannai (test)	11	0.44	97.21
Diatom frustrules	9	0.36	97.57
T. sp. B	7	0.28	97.85
Foraminiferan sp. (test)	6	0.24	98.09
Textularia sp. (test)	6	0.24	98.33
Faujacina sp.	5	0.20	98.53
Nonion sp. D	5	0.20	98.73
Triloculina sp. C	5	0.20	98.92
Rotorbinella sp.	4	0.16	99.08
Astrorhizidae sp.	3	0.12	99.20
Nonionella stella (test)	3	0.12	99.32
Cibicides sp.	2	0.08	99.40
Globobulimina sp.	2	0.08	99.48
Black spherules	1	0.04	99.52
B. sp. C (test)	1	0.04	99.56
B. sp. D (test)	1	0.04	99.60
Discorbinella sp.	1	0.04	99.64
Haplophragmoides sp.	1	0.04	99.68
Lagena sp. D	1	0.04	99.72
Ostracod valve	1	0.04	99.76
Rheophax sp.	1	0.04	99.80
Sacculina sp.	1	0.04	99.84
Sediment bolus	1	0.04	99.88
Spirulina sp.	1	0.04	99.92
Uvigerina sp. (test)	1	0.04	99.96
Virulina sp.	1	0.04	100.00
TOTAL = 47 TAXA	2511		

Appendix Table 2. Gut contents of 231 *Dentalium rectius* [144 (=62.3%) feeding].

Buccal Contents	Total	Percent	
		Item	Cumulative
Cribrononion lene	132	20.18	20.18
Sediment bolus	96	14.68	34.86
Mite eggs	64	9.79	44.65
Fecal pellet	42	6.42	51.07
Foraminiferan fragment	41	6.27	57.34
Florilus basispinatus	38	5.81	63.15
Mineral grains	37	5.66	68.81
Rosalina columbiensis (test)	22	3.36	72.17
Buliminella elegantissima	15	2.29	74.46
R. columbiensis	15	2.29	76.76
Cribrononion lene (test)	14	2.14	78.90
F. basispinatus (test)	14	2.14	81.04
Arthropod cuticle	11	1.68	82.72
Elphidiella hannai	11	1.68	84.40
Black spherules	7	1.07	85.47
Kinorhynch sp.	7	1.07	86.54
B. elegantissima (test)	6	0.92	87.46
Globobulimina sp.	6	0.92	88.38
B. exilis	5	0.76	89.14
Foraminiferan sp.	5	0.76	89.91
Ostracod valve	5	0.76	90.67
Rhizzamidae sp.	5	0.76	91.44
Astrorhizidae sp.	4	0.61	92.05
Nonionella stella	4	0.61	92.66
Unidentified turbellarian	4	0.61	93.27
Bivalve sp.	3	0.46	93.73
Bivalve valve	3	0.46	94.19
Clear eggs	3	0.46	94.65
Uvigerina sp.	3	0.46	95.11
Brisaster latifrons ossicle	2	0.31	95.41
Flintia sp.	2	0.31	95.72
Globobulimina sp. test	2	0.31	96.02
Haplophragmoides sp.	2	0.31	96.33
Ostracod sp.	2	0.31	96.64
Unidentified planulae	2	0.31	96.94
Sacculina sp.	2	0.31	97.25
Annulated object	1	0.15	97.40
Barnacle cyprid	1	0.15	97.55
Bryozoan statoblast	1	0.15	97.71
Buliminella exilis (test)	1	0.15	97.86
Cibicides sp.	1	0.15	98.01
E. hannai (test)	1	0.15	98.17
Gastropod eggs	1	0.15	98.32
Unidentified mite	1	0.15	98.47
Mollusk shell	1	0.15	98.62
Nonion sp.	1	0.15	98.78
Pegiidae sp.	1	0.15	98.93
Plastic rope	1	0.15	99.08
Polychaete setae	1	0.15	99.24
Textularia sp.	1	0.15	99.39
Triloculina sp. B	1	0.15	99.54
T. sp. C	1	0.15	99.69
T. sp. A	1	0.15	99.85
Foraminiferan test	1	0.15	100.00
TOTAL = 34 TAXA	654		

Appendix Table 3. Buccal contents of 149 *Pulsellum salishorum* [102 (=68.4%) feeding].

Buccal Contents	Total	Percent	
		Item	Cumulative
Cribonion lene	210	34.83	34.83
Foraminiferan fragment	113	18.74	53.57
Foraminiferan test	45	7.46	61.03
Unidentified foraminiferan	37	6.14	67.16
Mineral grains	35	5.80	72.97
Elphidiella hannai	25	4.15	77.11
Rosalina columbiensis	21	3.48	80.60
Florilus basispinatus	18	2.99	83.58
C. lene (test)	14	2.32	85.90
R. columbiensis (test)	12	1.99	87.89
Buliminella exilis	10	1.66	89.55
Sediment bolus	7	1.16	90.71
Nonionella stella	6	1.00	91.71
Sacculina sp.	6	1.00	92.70
Black spherules	5	0.83	93.53
Triloculina sp. A	5	0.83	94.36
B. elegantissima	4	0.66	95.02
Rotorbinella sp.	4	0.66	95.69
Uvigerina sp.	4	0.66	96.35
B. sp. C	3	0.50	96.85
Fecal pellet	3	0.50	97.35
Mite eggs	3	0.50	97.84
B. elegantissima (test)	2	0.33	98..18
B. exilis (test)	2	0.33	98.51
F. basispinatus test	2	0.33	98.84
N. stella	2	0.33	99.17
Dsicorbinella sp.	1	0.17	99.34
Faujacina sp.	1	0.17	99.50
Pegiidae sp.	1	0.17	99.67
Rotorbinella sp. (test)	1	0.17	99.83
Textularia sp.	1	0.17	100.00
TOTAL = 31 TAXA	603		

FINANCIAL REPORT

REPORT OF THE TREASURER FOR THE FISCAL YEAR ENDING DECEMBER 31, 1988

ASSETS			
Current Assets			
AMU Operating Acc. No. 3400934	$ 9,208.02		
Fortune Federal/C.D. No. 0203206756	4,068.57		
Fortune Federal/C.D. No. 0203206757	2,642.47		
Fortune Federal/C.D. No. 0203127749	6,289.05		
Fortune Federal/C.D. No. 0433212265	22,710.51		
San Antonio Acc. No. 680005702	3,640.26		
American Life & Casualty Ins. Co.	14,109.98		
Community Bank of the Islands	4,912.65		
Total Current Assets		$67,581.51	
Other Assets	.00		
Total Other Assets		.00	
Total Assets			$67,581.51
LIABILITIES AND EQUITY			
Current Liabilities			
Total Liabilities		.00	
Equity			
Retained Earnings	$68,696.11		
Net Income (Loss)	1,114.60		
Total Equity		$67,581.51	
Total Liability and Equity			$67,581.51

	Current-Period Amount	Year-to-Date Amount
RECEIPTS:		
Memberships		
Regular	$ 57.50	$10,469.50
Life	.00	288.50
Sustaining	.00	135.00
Student (Regular)	30.00	537.00
Student (Foreign)	.00	22.50
Corresponding	26.00	1,093.39
Clubs	22.00	730.00
Institutions	550.00	1,972.00
Total Membership Receipts	685.50	15,247.89
Sales		
Bulletin/Back Copies	.00	1,582.89
Bulletin/Special Edition	.00	938.00
Bulletin/Page Charges	.00	393.00
Bulletin/Reprint	.00	1,606.25
How to Study and Collect Shells	.00	135.25
Total Sales Receipts	.00	4,655.76

Other Sales Receipts		
Endowment Fund Donations	.00	5,078.65
Interest on All Accounts	3,835.00	4,853.60
Miscellaneous Donations	.00	342.39
AMU Registration/Meeting	.00	1,990.79
Separates	.00	279.23
Total Other Sales Receipts	3,835.00	12,544.66
Total Cash Receipts	$ 4,520.50	$32,448.31
DISBURSEMENTS		
Bulletin/Expenses	.00	
Bulletin/Postage	.00	1,286.09
Bulletin/Printing	.00	19,031.36
AMU Newsletter/Postage	.00	213.21
AMU Newsletter/Printing	.00	4,212.37
AMU Newsletter/Expenses	.00	351.37
Other Postage	.00	500.75
Other Printing	.00	112.65
Office Supplies	.00	417.07
Dues	.00	610.00
Officer's Travel	.00	2,000.00
Accounting	.00	300.00
Filing Fee (California)	.00	32.50
Symposium Endowment Fund Dep.	.00	2,100.00
Student Awards	.00	750.00
Insurance	.00	199.00
Bank Charges	.00	32.50
Miscellaneous/Petty Cash	.00	882.22
AMU Meeting	.00	532.00
Total Disbursements	.00	$33,562.91
Net Income (Loss)	$ 4,520.50	($ 1,114.60)

56th ANNUAL MEETING
THE AMERICAN MALACOLOGICAL UNION
WOODS HOLE, MASSACHUSETTS
JUNE 3 - 7, 1990

The 56th annual meeting of the AMU will be held from 3-7 June 1990 at the Marine Biological Laboratory (MBL) in the village of Woods Hole, Massachusetts on Cape Cod. The MBL recently celebrated its Centennial and has a distinguished history of research on molluscs. Its library (to which all registrants will have free access) is considered one of the best in the world. Woods Hole is also the home of the Woods Hole Oceanographic Institution (WHOI), National Marine Fisheries Service (NMFS), U.S. Geological Survey and Sea Education Associates.

Woods Hole is accessible by excellent bus service or by car from Boston or Providence, R.I. (each 70 miles); the nearest major airport is in Boston. Discounted air transportation can be coordinated, free of charge, through Rhodes Travel (1-800-356-6008). Dormitories (for students only) and motel accommodations are available in Woods Hole, and a very reasonable cafeteria meal plan will be available on campus during the meeting.

Two symposia are planned:

THE BEHAVIOR OF MOLLUSCS
With special session on Integrative Neurobiology and Behavior, round-table
discussion on evolutionary aspects of behavior, and a film festival
(Organized by Dr. Roger T. Hanlon)

SYSTEMATICS, BIOLOGY AND FISHERIES OF RECENT CEPHALOPODS
in honor of the late Professor Gilbert L. Voss
(Organized by Dr. Clyde F. E. Roper)

In addition to the symposia, contributed papers and poster presentations, scheduled events will include a workshop on home aquaria, a marine collecting trip on the MBL vessel in Vineyard Sound, shore trips to collect and observe intertidal molluscs, trips to the NMFS Aquarium, WHOI, Boston Aquarium and the National Seashore, plus an auction, outdoor clam bake and a banquet.

Vacation opportunities abound throughout Cape Cod. The ferry to Martha's Vineyard and Nantucket is located in Woods Hole. Weather in early June is likely to be quite cool.

For further information please contact:

Roger T. Hanlon
President, AMU
The Marine Biomedical Institute
The University of Texas Medical Branch
Galveston, Texas 77550-2772

Telephone (409) 761-2133
FAX (409) 762-9382

AMERICAN MUSEUM OF NATURAL HISTORY FELLOWSHIPS

FELLOWSHIPS - American Museum of Natural History Research /Museum Fellowships are available to postdoctoral researchers and established scholars starting in summer and fall 1990. Deadline for applications is January 15, 1990.

GRANTS - Grants are available to advanced predoctoral candidates and recent postdoctoral researchers. Awards range from $200 - $1,000. Deadlines vary according to grant program:

- ★ Theodore Roosevelt (N.A. fauna) - February 15, 1990
- ★ Lerner-Gray (marine) - March 15, 1990.

Request information booklet and applications from the Office of Grants and Fellowships, Department I, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A.

EXOTIC BIVALVE SYMPOSIUM

In conjunction with the Annual Meeting of the American Society of Limnology and Oceanography (ASLO) to be held in Williamsburg, Virginia, U.S.A., from 10-14 June 1990, a special symposium examining the distribution, physiology, and ecosystem role of the Asiatic clam, *Corbicula fluminea*, and European zebra mussel, *Dreisenna polymorpha*, will be held. Approximately 20 papers will be presented. Other special sessions or symposia at the ASLO meeting will include Eutrophication of Estuaries, Spring Phytoplankton Blooms, Global Climate Change, Turbidity Dynamics in Freshwater and Marine Systems, and Extracellular Enzyme Activities in Aquatic Ecosystems. For further information on the Exotic Bivalve Symposium, contact Thomas Crisman/Robert Brock (904-392-0838) or Renata Claudi (416-592-4163).

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Dates of Publication

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CONTRIBUTOR INFORMATION

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Seed. R. 1980. Shell growth and form in the Bivalvia. *In: Skeletal Growth of Aquatic Organisms,* D. C. Rhoads and R. A. Lutz, eds. pp. 23-67. Plenum Press, New York.

Vail, V. A. 1977. Comparative reproductive anatomy of 3 viviparid gastropods. *Malacologia* 16(2):519-540.

Yonge, C. M. and T. E. Thompson. 1976. *Living Marine Molluscs.* William Collins Sons & Co., Ltd., London. 288 pp.

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